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THE UNIVERSITY OF ALBERTA

ON PHYTOLITHS, LATE QUATERNARY ECOLOGY OF BERINGIA, AND INFORMATION EVOLUTIONARY THEORY

by

MIGUEL BOMBIN

A THESIS

SUBMITTED TO THE FACULTY OF GRADUATE STUDIES AND RESEARCH

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ABSTRACT

The history and state of the art of phytolith analysis is critically reviewed. New techniques for collection of samples, processing, mounting, and optical and SEM microscopic analyses are presented. An innovative approach to grass and sedge phytolith taxonomy is proposed within an ontogenic and anatomical framework. Applications and avenues for phytolith research are indicated.

Conflicting hypotheses about the Quaternary (Pleistocene-Holocene mesoglacial) paleobiology of Beringia are tested for the first time by phytolith analysis. It is shown that fossil phytoliths are abundant and widespread in Beringian lake sediments, muck, and coprolites. Preliminary results indicate that the physiognomy of the plant cover during the last glacial and mesoglacial (corresponding to the regional herb pollen zone), is better described by a vegetation mosaic, where probably diverse steppes were important components. These steppes would have included graminoid elements that occur today in more southerly temperate habitats. Phytolith data confirms the carbon stable isotope indication that C_4 plants were not a feature of the herb zone steppes. Different grass-rich assemblages continued to be widespread in Alaska and the Yukon throughout the mesoglacial (at least up to about 8,000 BP). This could have important paleobiological and archaeological implications.

It is proposed, in an extended note, that under natural conditions evolution is a stochastic process that produces genetic information heterogeneity selected in hierarchical sets of higher internal information redundancy. Therefore, selection would be a result, and not a cause of evolution. It is also suggested that the fundamental mechanism of evolution is the change in transition information (transition probabilities) of ontogenic chains. If transition probabilities change along ontogenic epigenetic chains, evolution will be translated into topological transformations of the descendents. If information is added or subtracted along the chains, or splitted (change in number of possible transitions at any state of the chain), it will be translated into topological jumps. In each of the two cases there is a change in one of the two constants of the capacity of information equation (allometric equation). Cultural evolution, being a different process, cannot be equated to biological evolution. A variety of new and reinterpreted concepts is also presented in the same note, to serve as a framework for evolutionary theory, particularly on: information theory, mind, culture, and niche. In another extended note, the subject of megafaunal extinctions in the New World is reinterpreted, an it is concluded that this episode is better modeled by a combination of interrelated feedback processes, in which anthropogenic effects are prominent.

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1. Overture

I am aware that most points of the thesis will benefit from expanded explanations and illustrations, and certainly everything in it can be improved with further work. However, at this point, I had to compromise between scope of content and a practical text size. Very often, I think, technical parts will be obvious only to the specialist, but, as a whole, I assume that its intended contribution would be comprehensible to any scholar. Work is still in progress, or is just beginning, on most of the subjects presented here. Thus, this should be considered, in general, as a first approximation to the topics herein.

The themes in this thesis stemmed from efforts to elucidate biological and anthropological problems under a unitary theoretical framework, and a perspective with time depth. The main source of empirical data has been Quaternary evidence, including the present. My first observations on phytoliths were done about 10 years ago, when looking for microfossils that could be used to reconstruct the Late Quaternary paleoecology of an area in southeastern South America (Bombin, 1976). The sediments of the Touro Passo Formation in that region were poor in pollen, but very rich in the intriguing silica bodies, which later became the focus of my research for this thesis. My involvement with the anatomical study of phytoliths and their ontogeny were also the germ for the evolutionary ideas presented in Note 1.

This opus is intended as a multivariate contribution to evolutionary, ecological, and anthropological theory and method, and also to demonstrate their application to problem-solving in Quaternary research. As a whole, it illustrates the operation and synergy of holistic thinking when addressing lingering interdisciplinary questions, as well as the effect of introducing innovative theory and new techniques to interpret Natural History.

Quaternary studies have developed into a very broad and interdisciplinary area of intellectual endeavor. Figure 1 shows the tetrad of sciences and arts that form the basis for understanding the history and processes operating on Earth during the last 2 million years or so. At the base of the tetrahedron stand the natural sciences; at the apex of it are the sciences related to the most distinctive of human traits, culture, and also the arts and philosophy. The tetrahedron is immersed in the media used to express information, which can be a spoken language, a computer language, mathematical language, or all. Quaternary studies are indeed diverse. Attending a meeting of Quaternarists, for example, one finds people from departments as varied as anthropology, biology, geology, geography, physics, chemistry, history, and so on. The papers they deliver might be even more diverse, from isotopes, to geomorphology, soils, and sediments; or from biological extinctions, human evolution, pollen and snails, to origins of agriculture, fire, prehistoric art, or the climato-ergotic reasons for

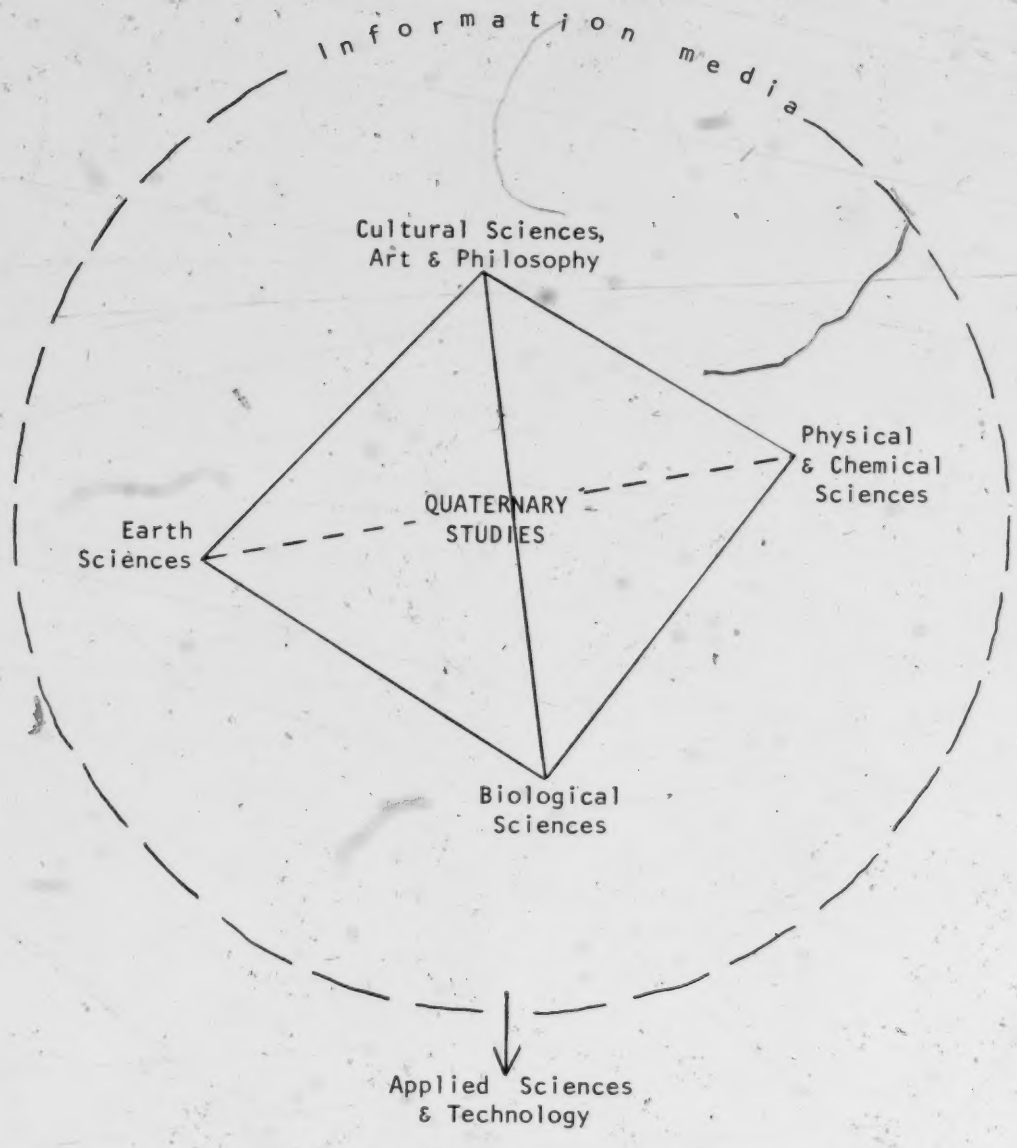


Figure 1 - Interdisciplinary position of Quaternary studies among the sciences, art, and philosophy.

the paintings of Hieronymus Bosch. Quaternary research also contributes to applied sciences such as engineering, agriculture, and natural resource management.

Why is it so interesting to rummage into the Quaternary? Principally because its recentness, in geological time, provides the richest testimony of and the basis to understand and reconstruct the past history of Earth. It also leads to clues to explain the present, and extrapolate the future. In particular, it yields scenarios of our own paleoecology and evolution.

However, because the record is so fresh, strict uniformitarianism is a common assumption in Quaternary paleoecology that needs to be challenged. Many ecosystems, even of the recent geological past, have no counterpart in the present, because of the so many different possible qualitative and quantitative combinations of organismic and environmental matrices. For example, there is nothing today in the New World comparable to an ecosystem containing elephants, horses, camels, ground sloths, etc., and lacking humans, which was a common combination in the Late Pleistocene of this continent.

The success of Quaternary research is directly dependent upon the adequacy of theory and methods derived from the sciences and arts that supply ways of testing its hypotheses, and solving its problems. In particular, time scales and resolution have to be appropriate in the search for correlations and cause-effect explanations.

On the other hand, Quaternarists can actually help identifying the need for new theory in the basic sciences, as in the case of Clementian versus Gleasonian views, and new methods, as in the case of pollen analysis. There are fundamental points in biology and anthropology that need refreshing of concepts and new theory, principally on evolution, culture, and the role of information. And there is always the opportunity to introduce or develop new techniques, to advance or refine the knowledge about our geological period. The use of stable isotope (Note 4) and phytolith analyses (chapters 2 and 3) are but two of such instances.

In summary, the objectives of this thesis are:

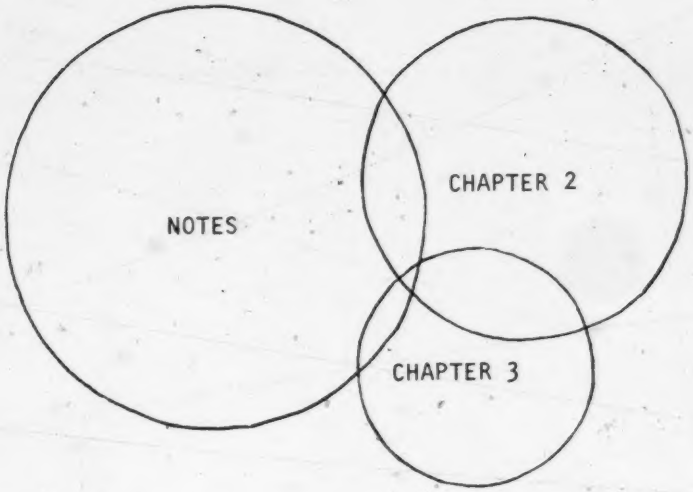
a) Introduce innovations and a fresh approach to the method of phytolith analysis, within the framework of plant anatomy, ontogeny, and new theory.

b) Apply the new developments in theory and method of phytolith analysis to test specific hypotheses on the ecology of Beringia at the critical time of human arrival to the New World.

c) Present unifying new evolutionary and ecological theory based on informatics, of interdisciplinary interest to anthropology and biology; as well as provide an explanatory model for the extinction of megamammals during the American Pleisto-Holocene **mesoglacial** (i.e. transitional period from full glacial to full interglacial mode).

Basically, the subject of Note 1 is on general theory, and as such, it will hopefully find applications in other subjects not covered by this work, and possibly contribute to modify current evolutionary thinking. Here it serves specifically as a theoretical framework, and to spell general hypotheses in part tested by cases presented in chapters 2 and 3, which, in turn, will provide strength to the theory.

The subject of chapter 2 (phytolith analysis), will also find applications in wide ranging studies. Here, it paves the way to understand its use in testing particular hypotheses and reconstructing Beringian paleoenvironments, which are the central topics of chapter 3. The material presented on evolutionary and ecological theory, paleoenvironmental modeling (with phytoliths and other methods), and Beringian paleobiology, are all fundamental to understand my view on the problem of mesoglacial megafaunal extinctions in the New World, dealt with in Note 5. Adapted versions of chapters 2, 3, and the extended notes 1 and 5 will be submitted for publication as separate but related papers. The Venn and cluster diagrams in Figure 2 illustrate graphically the relationships among the different parts of the thesis.



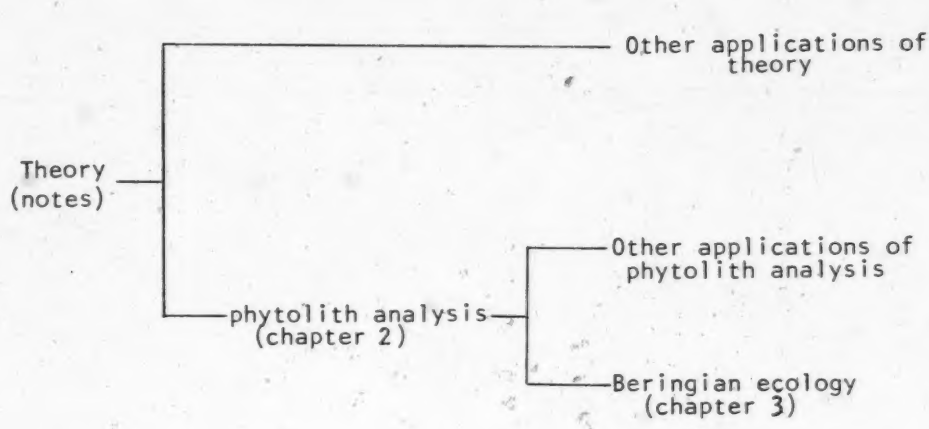


Figure 2 - Relationship amongst the parts of the thesis.

2. Phytolith Analysis: a New Beginning

2.1 Avant propos

Phytoliths are intracellular siliceous corpuscles deposited in a variety of plants. **Phytolith analysis** is the decodification of evolutionary, ecological, or any other information from phytoliths.

The development of phytolith analysis started some 140 years ago, but its progress has been incredibly slow in comparison to other parallel methods, such as pollen and diatom analyses. Moreover, most phytolith research has followed the same unfruitful pathways again and again. The result is that phytoliths are so obscure as not to be included in dictionaries such as Webster and Oxford (where only the outdated meaning of the word, plant fossils, is given), and phytolith analysis is so low key among the arsenal of paleoecological tools as not to be included at all, or given two incorrect lines in modern textbooks (e.g. Birks & Birks, 1980). Perhaps even more inconceivable is the fact that phytoliths are not mentioned at all in a recent review of paleoagrostology by Thomasson (1980).

The only way to elevate the method to its potential status is to attempt a new beginning. Therefore, the objective of this chapter is not to provide an extensive review of previous work on phytoliths, but rather to present what I think is essentially needed to practice the method, as well as a summary of the different perspective and

innovative ideas that I have been developing in the last 10 years. These are, in general, radically distinctive from the currently published state of the art. In large extent it relies theoretically on ideas presented in Note 1, and serves as basis for chapter 3. The reader interested in the traditional and presently main stream approach to phytolith analysis, will find reviews in Bertoldi de Pomar (1975), Bonnett (1972), Deflandre (1963), Geis and Jones (1973), Laroche (1977), Norgren (1973), Pearsall (1982), Piperno (1983), Rovner (1971, 1983), and Taugourdeau-Lantz *et al.* (1976).

If future historians of phytolith analysis consider the innovations presented here as a turning point, which precipitated the extinction of the present main stream ways in phytolith analysis, the objectives of this chapter would have been accomplished.

2.2 Background

Bioliths are mineralized biological structures. Their presence in organisms contributes to physical properties such as structural strength, density and optical qualities as well as participates in mineral storage pools and metabolism, protection, and biogeochemical cycles. Paleontologically, bioliths are very important because they become fossils par excellence. In my view there are five kinds of bioliths: biocrystals, bioconcretions, agglutinoliths, hystoliths, and cytoliths.

Biocrystals are intracellular or extracellular, isolated or aggregated crystals. Oxalate and phosphate single crystals or druses are examples of this type of biolith.

Bioconcretions are interstitial mineral-organic depositions. Intercellular deposits, tabashir (biosilica concretions deposited within the hollow internodes of bamboos), calculi, and dental tartar exemplify this category. Some biocrystals and bioconcretions are pathological, as for example renal calculi and joint calcium pyrophosphate crystals.

Agglutinoliths result from the agglutination of mineral particles by an organic matrix. Tintinnid, Rhizopoda, and some foram tests, or some worm tubes are examples of these bioliths.

Histoliths are mineralized tissue such as bone, teeth, invertebrate shells and exoskeletons, radulas, cuttlebones, otoliths, scales, scolecodont and worm jaws, conodonts, oogonia (e.g. *Chara*), some worm tubes, and calcified tissues.

Cytoliths are mineralized cells or cellular structures. They can be subdivided according to their taxonomic origin into zooliths, thecaliths, and phytoliths. **Zooliths** are animal cytoliths, e.g. sponge and octocoral spicules. **Thecaliths** are cytoliths derived from protists, such as forams, thecamebae, Chrysophyta, diatoms, radiolarians, silicoflagellates, and Coccolithophoridaceae.

Phytoliths, the cytoliths object of this chapter, are diversely shaped silica corpuscles formed within a variety of plant cells. Although in the literature other mineralized plant structures are sometimes classified as phytoliths, the usage of the restricted definition above is recommended on natural and practical grounds.

Biosilica is largely the chief component of phytoliths, usually with an organic matrix and/or inclusions. Biosilica results from the polymerization of $Si(OH)_4$ (monosilicic acid) in biofluids, through the formation of Si-O covalent bonds. It varies from a rigid silicagel to a hydrated opaline amorphous or very poorly crystalized form of silica. The chemical conditions within the plant for polymerization are silicic acid concentration around 100-300 ppm and pH neutral to basic. The presence of hydroxyl groups on the outside of the biosilica polymers, creates a surface of points favorable to hydrogen bonding (e.g. with water or other polar molecules such as carbohydrates and proteins), or even substitution of the hydroxyl H for cations. The cations of Na, K, Li, Ca, Mg, Fe, Cu, Mn, Al, and Ti were already identified in phytoliths (Bertoldi de Pomar, 1975, compiled a list from several references).

The silica polymers (primary structure) grow to form spherules from 10 to 3,500 Å in diameter (secondary structure). Phytoliths are formed by packing of silica spherules (tertiary structure) directed by polar surfaces (cell walls, fibrils), or by self-packing. In both cases

they are not as closely packed as precious opal, producing a very porous structure (Peinemann & Ferreiro, 1972, report a specific surface of 122.4 m^2/g for phytoliths). The details of this process are discussed in section 2.4.

The size of known phytoliths varies from around 3 to 2000 µm. However, the overwhelming majority of phytoliths falls between 5 and 150 µm, that is in the silt and very fine sand range.

Phytoliths are usually transparent *in vivo*, and in many cases as fossils. They can be also translucent or opaque, depending on organic and other inclusions, corrosion, and staining. Their index of refraction varies from 1.40 to 1.47, and they are usually isotropic and non-birefringent.

The density of phytoliths varies between 1.5 and 2.3 g/cm^3, with an average around 2.10 and 2.15 g/cm^3. This variability is due to differences in porosity, hydration, inclusions, lacunae, and vacuoles. Decay of phytoliths is a source of soluble silica to the biogeochemical cycle of silicon, but depending upon the diagenetic conditions they can be quite durable as fossils (comparable to diatoms, radiolarians, or any other biosiliceous structure). The solubility of phytoliths is largely unaffected by pH changes between 1 and 9, which is within the range of most soils and sediments; however, above pH 9 the solubility of phytoliths (and any other biosilica) increases very rapidly. Metallic ions attached to the surface of phytoliths during diagenesis, particularly of Al and Fe, inhibit their

dissolution due to the formation of insoluble silicate coatings. Preservation of phytoliths is best in amorphous silica rich soils or sediments, such as those including volcanic ash or abundant diatoms.

The properties above are generally favorable to phytolith preservation as fossils (the oldest phytoliths that I have observed come from the Upper Cretaceous, and older will no doubt be found), and to analysis (see section 2.3). More details about biogenic silica properties and related references are given by Wilding *et al.* (1977).

Phytoliths are notedly conspicuous among the monocots, particularly grasses, sedges, and palms. However, they occur thoughout the Plant Kingdom. A listing of plants containing biosilica is given by Voronkov *et al.* (1975).

The anatomical distribution of phytoliths is not absolutely constant in plants that produce them. Some cells are always silicified, for instance silica-cells of grasses, but with the exception of embryonic or meristematic cells, any type of cell can eventually silicify in phytolith-producing plants. In general the epidermis is richer in phytoliths, particularly in older cells subjected to higher transpiration.

Silica accumulation in plants can be very high, for example in *Equisetum*, where about 30% of its dry weight and more than 95% of the ash weight is silica. About 95% of the dry weight of ash from rice seed hulls is biosilica, and in Japan they are even used as a source of pure silicon for

electronics, solar cells (Amick, 1982), and other applications, as well as to produce cement. The average percentage of phytoliths per dry weight of grass leaves is about 1 to 5%. This means that a considerable amount of biogenic silica is incorporated in soils and sediments every year.

Upper horizons of soils under grassland vegetation usually contain from 0.1 to 10% of phytoliths by weight. I have analyzed soils and sediments from the Argentinian Pampa with up to 20% of phytoliths (up to 70% of the silt fraction), and Riquier (1960) reports on soils horizons of the Reunion Islands composed almost entirely by phytoliths.

As already discovered by Darwin and Ehrenberg last century, phytoliths are an important component of atmospheric dust. Baker (1960b), Folger *et al.* (1967), Parmenter and Folger (1974), Salgado-Labouriau (1978), and Suess (1966), present interesting data in connection with phytoliths in athmospheric dust.

As a matter of fact, since Ehrenberg (1843, 1854) many other authors have shown these silica bodies to be so widespread in soils, archaeological, and geological deposits, even in marine sediments (Bukry, 1979a, 1979b, 1980a, 1980b), covering at least the Upper Mesozoic and all the Cenozoic, that it is perplexing why their potential as fossils has not been as yet adequately explored (some of the possible reasons are discussed in section 2.2). Other sources of fossil phytoliths are coprolites and tartar

incrustations on vertebrate teeth (e.g. Armitage, 1975).

In accordance to theory presented in chapter 2, phytoliths should not be seen as an evolutionary adaptation to certain "selective pressures", for example as an anti-herbivore defense. Functions do not create structures; it is the other way around: structures create functional probabilities. The evolution of phytoliths generated a new parameter in the niches of their bearers, whether or not this changed significantly their probabilities of extinction is not clear yet.

In reality, the anti-herbivore hypothesis is at odds with the fact that plants such as grasses actually benefit from grazing (Estes *et al.*, 1982). Herbivores have more damage caused to their teeth by mineral dust and soil particles than by phytoliths within plants. When two very similar species of herbivores are compared, one feeding predominantly on grasses and the other on phytolith poor plants (e.g. the hyraxes studied by Walker *et al.*, 1978), there is no significant difference in fitness. Phytoliths could have some deterrent effect upon very small herbivores such as insects, but this is insignificant when they occur in plagues, such as grasshoppers. In reality, grasshopper clipping to a certain extent might help grasses in natural grasslands to survive concomitant drought by reducing transpiration surface. In addition, palatability in grasses is not well correlated with lower phytolith content (lower organic roughage is more correlated).

Another hypothesis is that a function of phytoliths is to improve the use of light by photosynthetic chlorenchyma below the epidermis, by acting as "windows" (Kaufman *et al.*, 1981). Reviewing the abundance of phytoliths in plants from well irradiated versus shaded habitats, no correlation or even a positive correlation is found (desert grasses, for example, are always very rich in phytoliths). Also, a higher concentration of phytoliths in grasses occurs at the terminal portions of the grass blades, which are more exposed to light. Therefore, although phytoliths might in some circumstances improve advantageously transmission of light to cells below the epidermis, there is no evidence for the evolution of phytoliths as an adaptation for such function.

The deposition of phytoliths could be involved in biochemical pathways through the metabolism of silicic acid, similarly to what Werner (1977) has proposed for diatoms. However, this does not explain their anatomical position and morphological variation, and is at odds with their ontogenesis in cells under metabolic "degeneration" (see section 2.4).

The most commonly listed function of phytoliths is that of providing strength to the leaves, for which there is not much support either. In the case of grasses and sedges, which have leaves formed by longitudinal rows of cell "tubes", it is at least conceivable that phytoliths could help prevent the "buckling of shells" effect on these

"tubes" (David Murray, University of Alberta, personal communication). However, as a general rule, their strengthening effect on leaves is probably negligible in comparison with the structural strength provided by cell turgescence, fibers, and silicification of cell walls.

In conclusion, no adaptationist program explanation for the presence, abundance, and morphology of phytoliths seems adequate at present. The functions of phytoliths, when existent, appear to be circumstantial. However, this does not mean that phytoliths are not important as a source of proxi data through their redundancy in relation to the source plant, and environmental parameters during their deposition. A discussion on the applications and potential uses of phytolith analysis is presented in section 2.5, and should suffice to stress its significance.

2.3 Historical aspects

According to Frenguelli (1930), Saussure was the first to reveal the existence of silicified cells in plants in his "Recherches sur la Végétation", published in 1804. However, Davy (1814) mentions that he had been observing plant silica since 1798. In any case, at least from the early 1800's silica has been known to occur in plants. Some time later Struve (1835) indicated that plant silica had to be deposited from silica taken from soil solution, demonstrated that plant silica is rapidly solubilized by hot potassium hydroxide, and is insoluble in acids. He also combusted

plants and treated the residue with acid to study the "*sceleti silicei*" under the microscope (a precursor of the spodographic method), and provided illustrations of phytoliths in Spanish reed leaves.

The first analysis of phytoliths from soils and sediments (mainly from Brazil) was presented to the Berlin Academy of Sciences in 1841 by C.G. Ehrenberg (Ehrenberg, 1843). A facsimile of a plate from this historical work is reproduced in Figure 3. In this paper he also proposed formally for the first time the name **Phytolitharia**, and attempted their first classification. It was an artificial classification, which Ehrenberg emphasized would be provisional, until the source-plants could be demonstrated for each morphotype. Ehrenberg (1854) showed the ubiquitous distribution and provided profuse illustrations of phytoliths from samples collected all over the world. C.G. Ehrenberg should be therefore considered the founder of phytolith analysis (Note 1).

After the death of Ehrenberg botanists continued studying phytoliths in living plants, but the subject of phytoliths in soils and sediments was never heard again until the 1920's, when Frenguelli (1920, 1925, 1930) published his observations on Argentinian Cenozoic sediments. However, his papers being in Spanish and published in Argentina, received little or no attention in Europe and North America (which is actually a general phenomenon with materials published outside the main

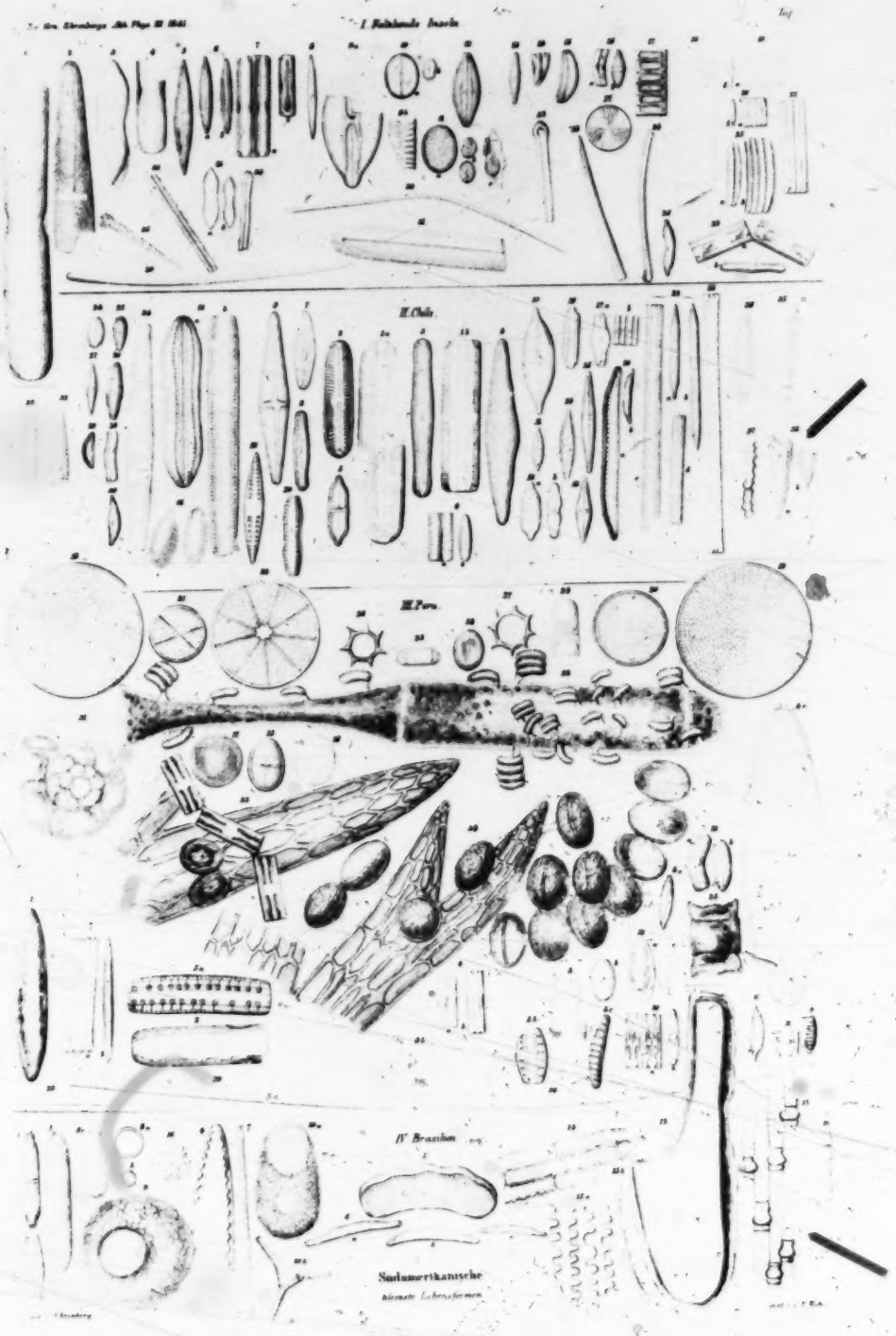


Figure 3 - Facsimile of a plate from Ehremberg's 1843 publication (his first illustration of phytoliths).

scientific "spheres of influence").

With the exception of a few citations by soil scientists, another gap in the literature about fossil phytoliths occurs between 1930 and 1956. Smithson (1956) was the starting point of a "bloom" of papers and theses on phytoliths by soil scientists, which lasted until the 1970's. Phytoliths in sediments also received some attention during this same period. Since then, the interest on soil phytoliths seems to have subsided.

The paper by Pearsall (1978), initiated a trend of interest in phytoliths from cultivated plants in archaeological contexts, and revived archaeologically oriented research on phytolith analysis. Irwin Rovner, of North Carolina State University, became the enthusiastic and energetic leader of this "renaissance", organizing several symposia since 1980, and starting the publication of the Phytolitharien Newsletter (P.O. Box 5535, Raleigh NC 27650, USA) in the fall of 1981. It is regrettable that such a praiseworthy effort produced so little new in phytolith research, because it is building upon an inadequate basis.

Many plant anatomical works since the last century include data about phytoliths (Netolitzky, 1929, summarizes the early work to that date), culminating with the monumental series "Anatomy of the Monocotyledons", edited by C.R. Metcalfe (of particular interest for phytolith analysis are Metcalfe, 1960, 1971). Recently, the monographies by Palmer and Tucker (1981, 1983), are examples of continuing

research in this area.

Another active line of research, started in the late sixties, is that of investigation of the epigenesis of silica deposition in plants, which is summarized in papers by Sangster and Parry (1981), and Kaufman *et al.* (1981).

The paper by Twiss *et al.* (1969), which is probably the most constant citation in phytolith analysis literature since it was published, is of historical interest for two reasons. First, because it must be said that it contains almost verbatim the classification proposed by Prat (1932, 1936, 1960), with additional information published by Metcalfe (1960). Actually Prat's classification is just a modified version of that available since Grob (1896). The paper by Twiss *et al.* having been published in an easily accessible and prestigious journal, it has been adopted as an original primary source, and so a classification known since last century in the literature in German and French, and later in English, became the "Twiss *et al.* classification." In the paper in question the authors base their classification on the observation of only 17 selected species of grasses. However, they cite Metcalfe (1960), which contains descriptions of hundreds of grasses, many of them the same or very similar to the ones studied by Twiss *et al.*. Second, because the classification is very crude and not universal, it has promoted innumerable mistakes in the literature. For example the classification all "dumbbell-shaped" phytoliths as panicoid, or all

"saddle-shaped" ones as chloridoid. The paper also induced researchers to regard elongated phytoliths as undiagnostic, and to restrict analyses to the superficial exercise of using phytoliths to identify sources at the subfamily level. In my opinion, the paper by Twiss *et al.* (1969), unfortunately canalized many years of unproductive research, helping to reinforce a negative, useless, and obscure image of phytolith analysis.

My view of the reasons for the stagnation and primitive state of the art in phytolith analysis can be summarized in three points:

a) Plant anatomists and taxonomists have usually only looked at phytoliths as curiosities, or as a secondary characteristic among many other more conspicuous morphological features of the living plant. Their work lacks an interdisciplinary perspective, therefore morphological details of isolated phytoliths, which are the vegetative part of the plant more commonly (usually the only one) preserved in Cenozoic soils and sediments, were never studied. Their absence of interest in phytoliths also helped create, and generalize the myth that isolated phytoliths are not taxonomically very diagnostic. Cellular biologists, again, were only interested in the processes of silica deposition without regard to morphology or paleobiological applications.

b) Soil scientists, sedimentologists, and archaeologists usually used artificial classifications, or

the simplistic classifications proposed by plant anatomists, which never advanced to much more than using such non-technical and imprecise terms as "hats", "dumbbells", "keystones", "hooks", and so on, to describe phytoliths. They also have not developed interdisciplinary connections. Plant anatomists and earth/soil scientists or archaeologists are perhaps more separated in universities, than physicists and economists. In addition, phytoliths still did not find applications in geological exploration and economic stratigraphy, the major pushing force towards the development of other micropaleontological fields such as stratigraphic palynology, diatom, foram, radiolarian, and silicoflagellate analyses, for example.

c) There is no comprehensive link between phytolith morphological properties and ecological, genetic, epigenetic, or evolutionary theory, which is a condition *sine qua non* to retrieve these interesting silica bodies from biological and scientific obscurantism.

In the next sections of this chapter and chapter 3 an attempt will be made to start eradication of the abovementioned problems.

2.4 Techniques

2.4.1 Collection of samples

I have collected soil and sediment samples for general phytolith analysis in the same way as any routine sampling

for micropaleontological analyses (Birks & Birks, 1980). The amount that I usually use for analysis is not more than 1 to 10 grams of sample; however, whenever possible I take a larger composite sample of 500-1000 g from a single stratigraphic unit, in case that concentration of rare phytoliths is necessary. The small sample can be obtained from this larger one after thorough homogenization. No special storage conditions are required, because phytoliths are not attacked by any known microorganism; however, dry samples are recommended for permanent storage, to minimize possible solubilization of biosilica. Contamination problems are usually not so crucial as in the case of pollen samples, because in general phytoliths are not so abundant or easily transported in the atmosphere.

Collection of samples to solve specific problems, e.g. archaeological features, should be tailor-made for each case. I suggest that the following should be always sampled for immediate or eventual phytolith analysis: ashes from archaeological sites, sediment adhered to archaeological artifacts, sediment from abdominal area of articulated fossil herbivore skeletons, sediment and concretions from fossil teeth, because all of those could potentially provide important paleoecological information.

Present soil, for reference or genesis studies, should be sampled to best represent the respective pedon. Reference samples from plant material may be collected fresh or from herbaria, because phytolith morphology is not altered by

drying. In theory all plant organs, including roots should be sampled. In practice, and for paleoecological purposes, the leaves being the part that produces most of the fossil phytoliths, are my first choice if a comprehensive reference is not feasible. For grasses and sedges, if only a portion of the leaf can be sampled, the medial segment of the blade is recommended as more representative, according to my personal observations of around 300 species of grasses, and 100 species of sedges, representing all the tribes of these families. I have also found that a good collection of herbivore feces from an area produces an excellent complement to soil and plant reference samples, because of excellent preservation of phytoliths in feces (and coprolites), and the better representation of the species trophically important.

2.4.2 Processing of samples

The most widely used techniques for processing phytoliths are discussed in Rovner (1983). The extraction of phytoliths from soils and sediments is based in the separation of phytoliths from the mineral fraction by means of a heavy liquid, such as bromoform, or tetrabromoethane, adjusted to density 2.3 with any apolar solvent. Carbone (1977), has used a saturated solution of potassium and cadmium iodide, boiled down to density 2.3, as a heavy liquid. However, having experimented with all the processing techniques for phytolith analysis available in the

literature, I did not find any of them totally satisfactory, for a variety of reasons. The main problems are alteration of phytoliths, unnecessarily complicated and tedious procedures, and the use of hazardous and/or expensive chemicals (such as the heavy liquids mentioned above). Therefore, I have developed a different set of procedures aiming to maximize: effectiveness, simplicity, safety, and low cost. These originally devised techniques are described below.

2.4.2.1 Reference plants

a) Put pieces of plant material into small vials.

b) Add 30% hydrogen peroxide to half of the vials' volume to oxidize the organic matter.

c) Cover loosely with the lid (to allow gas pressure to escape). Lid should be preferably plastic, and not have any organic materials such as cork.

d) Let stand for 48 h, and observe daily from then on to determine when the diaphanization process is adequate to see phytoliths with transmitted light. This is usually attained when the plant fragments are white and transluscent. Swirling the vials gently from time to time accelerates the process.

e1) For histological preparation of leaves ("wet spodogram"), put wet diaphanized pieces on microscope slides and dissect the abaxial and adaxial epidermes with histological needles or sharp blade. Leave them to dry as extended as possible on the surface of slides or

coverslips.

e2) For isolated phytoliths, close the lid and shake the vial vigorously from time to time. Open the lid immediately after shaking to relieve pressure. Continue to shake intermittently until a loose whitish sediment of phytoliths and other cellular debris is formed (generally about a week). Pipette one or two drops of the sediment onto a coverslip, and distribute the sediment on its surface as homogeneously as possible, and let it dry (heating at 50-70 °C helps). Loose pieces of epidermis can be included with the sediment to aid understanding of the anatomical relations of phytoliths *in situ*.

f) In both cases (e1 and e2), mount the coverslip with a medium that has a refraction index (RI) different from phytoliths (RI of phytoliths is usually around 1.43). Hyrax resin (Custom Research and Development Inc.) is a an excellent mounting medium with RI 1.65. Canada balsam (RI 1.54) or similar can also be employed. Cell walls (RI approximately 1.56) are not very well observed with Canada balsam but are very clearly seen with Hyrax.

Staining of phytoliths can be obtained with the methods given by Dayanandan *et al.* (1983). However, this is totally unnecessary for phytolith analysis, if the proper mounting medium is used. Staining, although esthetically atractive, actually tends to obscure

surface details.

In a well homogenized reference preparation there will be phytoliths in different views, but a liquid medium can be used to move phytoliths in order to better observe their tridimensional morphology. Of the mounting media used in palynology, glycerol is not good (poor optical contrast), but silicone oil can be used (although its RI 1.4 does not produce a marked optical contrast). Water is also satisfactory for non-permanent preparations. Experimentation with other media is in progress. When using liquid media, the corners of the slide should be anchored with drops of nail polish. Store the slides horizontally in slide boxes or drawers.

Vials with the samples of isolated phytoliths can be stored indefinitely. Preferably do not let them dry out.

Some plants are harder to diaphanize because of the cutine waxes and oils. In these cases, a pre-treatment with xylene or benzene for a few hours before the oxidation with H_2O_2, improves the results considerably.

Peats, organic soil horizons, recent feces, and non-mineralized coprolites, can be processed in the same way described above for reference plants.

Although the waiting time to have the samples ready can take several days, in the long run the procedure can save time, due to the little manipulation involved and the large batches that can be processed each time. If an

urgent preparation is necessary chromic acid can be added slowly (it will effervesce) to the H_2O_2 and left to react for a few hours. Then samples are washed thoroughly by repeated centrifugation with distilled water.

Observation: Handle 30% hydrogen peroxide with care. Do not touch it with bare hands. If H_2O_2 accidentally enters in contact with your skin (or eyes), wash immediately and thoroughly. If this is done, a benign white discoloration will occur and remain for some time. Apply a protective skin cream or lotion. If contact is prolonged, severe burning can occur. Never mix 30% hydrogen peroxide with alkaline substances.

2.4.2.2 Soils and sediments

One is frequently confronted with the problem of testing sediments or soils for the presence of phytoliths. It can be very dissapointing to go through a time-consuming processing only to find out that the samples were sterile. Therefore, two procedures are presented here. One for a quick test of phytolith richness in samples, which can actually be carried out in the field; and another for complete processing of fossiliferous samples, which produces cleaner preparations. Both methods recover any biosilica microfossils present (e.g. diatoms, cysts, spiculae). The method is based on density separation using an

acidic solution of zinc bromide, which is prepared as follows:

Stir slowly 100 ml of concentrated HCl into 1 kg of $ZnBr_2$ (heat will be generated). Slowly and carefully add 200 ml of distilled water. Allow to cool at room temperature. Use small volumes of water to adjust density to 2.3-2.4 g/cm^3, which can be measured by weighing a known volume, using a densimeter, or a set of different density chips. A simple densimeter can be improvised by calibrating and marking a tall vial containing some lead spherules. Filter if contamination is suspected. Store in dark bottle. This solution can be reused by filtration and addition of more $ZnBr_2$ if necessary. It can get darker with use, but this does not alter its properties for separation. Avoid contact with skin (wash thoroughly if it happens).

Rapid processing

a) Put 1-2 cm^3 of each sample in small vials or centrifuge tubes.

b) Add 5-10 ml of zinc bromide solution to the vials/tubes.

c) Mix well with a rod or equivalent. There will be effervescence if carbonates are present. If effervescence is too strong, add the zinc bromide 1 ml at a time.

d) Put a stopper on each vial/tube. If there is effervescence, leave the stoppers loose to avoid building up of pressure.

e) Leave the vials stand for 24 h or centrifuge the tubes for 20 minutes at 2,500-3,000 rpm. If there is effervescence let it stop first.

f) Scoop (with a flat toothpick for example) or pipette one or two drops of the float and transfer to a slide, add a drop or two of the zinc bromide solution, homogenize (with the same toothpick), put a coverslip, wait until the liquid spreads between the slide and coverslip, and put a drop of nail polish on each corner of the coverslip to anchor.

If steps c, d, and e are repeated several times, a better recovery is obtained.

The use of the zinc bromide heavy liquid as a density separation agent, and as a mounting medium is very handy indeed. Three good properties of the zinc bromide as a mounting medium are: it does not dry out because $ZnBr_2$ is hygroscopic, the phytoliths remain closer to the coverslip making them easier to observe and move. Moving of phytoliths is easily accomplished by pressing gently any point of the coverslip with a pointed object (e.g. needle, pencil, toothpick). The RI is around 1.56, which is satisfactory for analysis of phytolith morphological features. Slides must be stored horizontally. Sometimes the results are so good that

analysis can be fully carried out on these preparations.

Full processing

a) Put 1-5 g of soil or sediment sample (usually dry and finely divided) in a tall 200 ml beaker or equivalent.

b) To disagreggate the sample, add 40-60 ml of acetate buffer (1 N sodium acetate solution adjusted to pH 5 with acetic acid), stirring frequently for 24-48 h. If there is not much carbonate in the sample this should be enough to disperse it. Ultrasonic vibration (20 KHz) can be used for very difficult cases, but normally it should not be necessary for unconsolidated samples. If the sample is very calcareous, decant and repeat treatment with acetate buffer until there is no more effervescence. If effervescence is too pronounced, it can be controlled by a jet of alcohol from a washing bottle. If the sample is too organic, a pre-treatment with 30% hydrogen peroxide might be necessary. If the sample is too rich in clay, add water to form a column of suspension 5 cm deep in the beaker, stir and let stand for 30 minutes, decant, and repeat if necessary several times (rarely the case).

c) Transfer to small centrifuge tubes using 10% HCl. Balance with 10% HCl. Centrifuge 5-10 min at 2,000-3,000 rpm. Decant.

d) Add 10-15 ml of zinc bromide to the tubes with centrifuged sample. Stir and shake well (use stopper) for a few minutes. Centrifuge at 2,000-3,000 rpm for 20 minutes. A better recovery of phytoliths is usually obtained if the tubes are stirred and centrifuged several times (with the same $ZnBr_2$ instead of repeating extraction with new $ZnBr_2$ and wasting heavy liquid solution).

A sample of the float can be mounted after this step, the same as in step f of the rapid processing method. The float and a portion of the clear column of heavy liquid below it can be transferred to a vial and stored until processing is continued.

"Absolute" phytolith counts or phytolith influx can be obtained the same way as pollen, by spiking the sediment with a known amount of contaminant (e.g. exotic pollen). Limited experimentation indicates that microspherules for column ionic exchange could be used as a contaminant.

e) Pippete the float to another centrifuge tube. Add 10% HCl to the float residue. Centrifuge and decant. Wash with distilled water twice or three times, transfer to a vial with water. The float can be also easily transferred to another centrifuge tube by freezing the bottom of the separation tube with liquid nitrogen.

f) Mount using the same procedure described in step e2 and f of the reference plants method.

Mounting samples for SEM Pipette 1 or 2 drops of sediment from processed sample (after step e2 for reference plants, and step f of the full processing method for soils/sediments) onto an aluminum SEM stub, homogenizing sample over the surface of the stub. Let dry at 60-70 °C for 24 h. Coat as usual for SEM just before analysis is to begin.

Pieces of leaves partially treated with H_2O_2 and dried, or simply just dry herbarium material can be mounted on stubs with double-coated Scotch tape, and coated as usual.

Examples of results obtained with my processing techniques are shown in the microphotographs of maize preparations represented in Figure 4.

2.4.3 Microscopy

Optical microscopic observation of phytoliths is normally done with a common compound biological microscope (the ideal being a trinocular with attachment and camera for microphotography). Routine counting is carried out at 400X (or at a maximum of 650X). Details rarely need to be observed by the use of immersion and 1000X. Petrographic microscopes, frequently cited in the literature about phytoliths as the instrument of choice, are not necessary, and some models are actually too cumbersome for the systematic counting of phytoliths. It is an advantage having polarizers to differentiate altered phytoliths from mineral

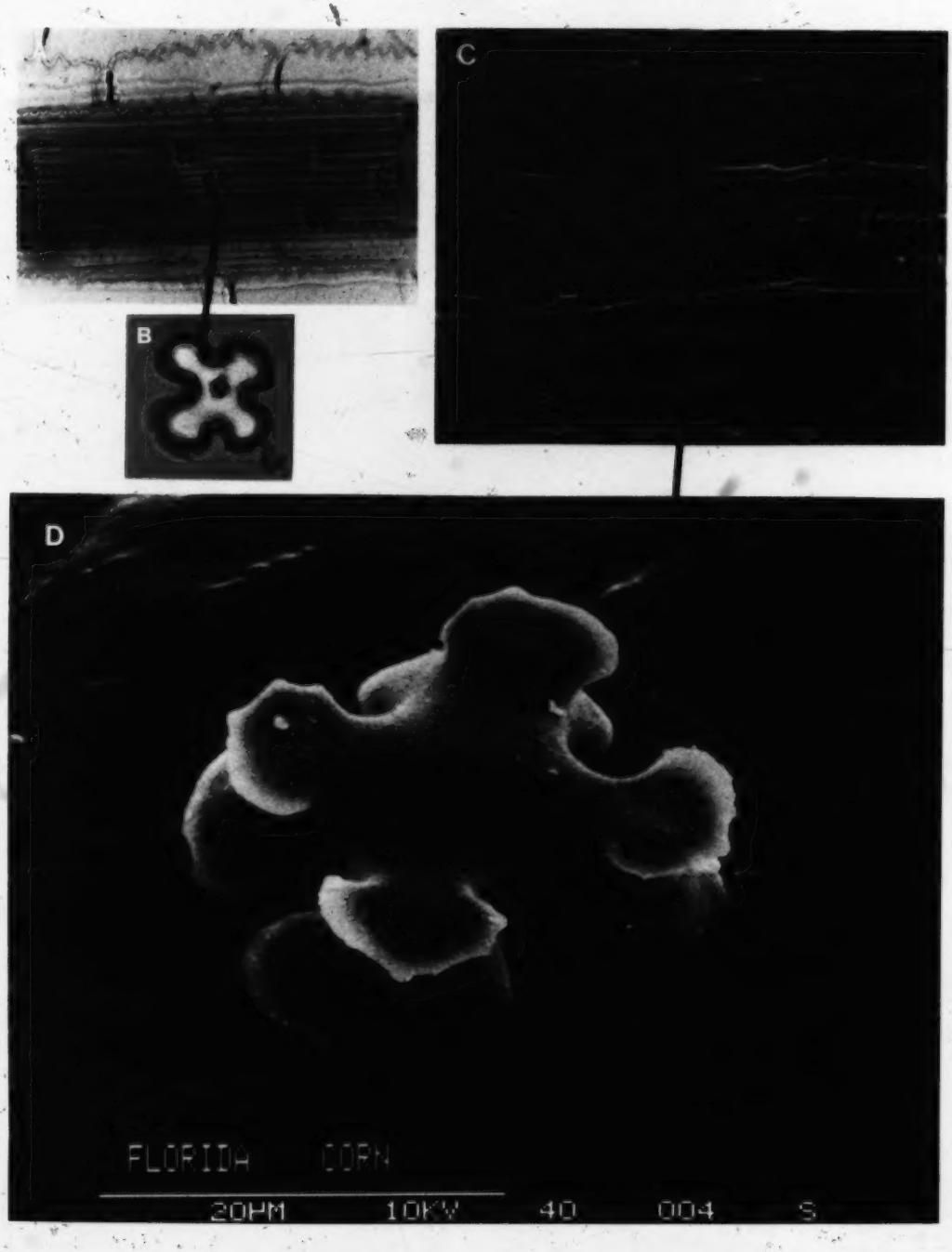


Figure 4 - Maize phytoliths. A: epidermal preparation, OM. B: isolated phytolith, OM. C: epidermal surface, SEM. D: isolated phytolith, SEM.

or other particles in some cases, but this can be easily improvised by using a pair of polarizers (e.g. from polarizing sunglasses). However, as a rule, if a microscopic particle cannot be identified as a phytolith with simple optics, probably it is not a phytolith or it is not worth counting. High resolution optics, interference, phase contrast, and other more sophisticated resources can be used occasionally if available, but they are certainly not necessary for basic research and routine analyses.

Phytolith counts should include a balanced number of fields from the borders, the middle, and the intermediate areas of the preparation, to minimize any biased distribution of phytoliths due to artifacts of mounting.

The numbers of phytoliths to be counted depends on the problem under investigation, the desired confidence intervals, and the diversity of the sample. For example, if only the presence of a certain kind of phytolith is important (e.g. maize in archaeological samples), the total number of phytoliths counted is not critical. For paleoenvironmental analyses, the problem is similar to that of pollen counts (Birks and Birks, 1980). By plotting the number of morphotypes encountered versus number of phytoliths counted of many different soil and sediment samples, it is suggested that a plateau of number of morphotypes is usually reached between 300 to 1000 phytoliths (median around 500 phytoliths). Therefore, empirically it seems reasonable to count around 500

phytoliths in each sample for routine quantitative paleoecological work. Counts smaller than 500 phytoliths can be statistically acceptable depending on their diversity (confidence intervals will help evaluating these results). Counts smaller than 300 phytoliths are also informative, but it is better to consider them as semi-quantitative (i.e. into classes such as none, rare, common, abundant) or even presence-absence counts.

SEM microscopy is not practical for routine identification and counting of phytoliths, due to the time and cost involved; however, it has a place in phytolith analysis to accomplish the following:

- Facilitate the translation of encoded information on tridimensional features of phytoliths for retrieval upon routine light microscopy.

- Provide the basis for more accurate taxonomy of phytoliths, and improve the information about their evolutionary relationships.

- Demonstrate tridimensional anatomical relations of phytoliths on the epidermal surface.

- Help understanding their ontogeny.

Any SEM model, even the simplest, can be used to study phytoliths. Stereopairs can be produced by taking two photographs of the same phytolith at a slightly different angle (e.g. 7°). If a X-ray microbeam energy dispersion unit linked to the SEM is available, complementary studies of silicification of cells, cell walls, and intercellular areas

can be accomplished by semi-quantitatively determining silicon. The siliceous nature of unusual morphotypes can also be confirmed by this analysis.

TEM finds application only in studies about the ontogenesis and ultramicroscopic development of phytoliths.

Finally, the underdevelopment of phytolith analysis cannot be atributed to technological barriers. The means for progress in phytolith analysis are all in place. Actually, basic and routine research in this area can be practiced with very limited resources anywhere in the world. The only prerequisite, then, is at the level of information. Next section is designed to supplement this area.

2.5 Ontogeny, anatomy, and taxonomy

Phytoliths result from silicification within different cells of plants, and each kind of cell varies morphologically along the spectra of plant taxa. Therefore, to reflect relations of natural information, a phytolith taxonomy should be firstly anatomical, and secondly morphological, representing both ontogenesis and evolutionary history. None of the published phytolith taxonomies (most refer to grasses) meets the requirements above.

Artificial classifications such as Ehrenberg (1843, 1854) or Bertoldi de Pomar (1975) could be applied for stratigraphic purposes, but are clearly unsatisfactory from a biological or paleobiological point of view. In addition,

Ehrenberg's classification (revived by Deflandre, 1963, and Dumitrica, 1973) is certainly obsolete. The taxonomic attempt by Bertoldi de Pomar (1975), which I actually employed in earlier work (e.g. Bombin, 1976, 1980a), contains errors, such as: dividing the phytoliths in microphytoliths (smaller than 40 micrometers) and macrophytoliths (larger than 40 micrometers); including crescent shaped and dumbbell shaped phytoliths in the same category; and lateral views of phytoliths as a separate category ("estrobilolita").

Of the available anatomical classifications, some are too crude and ambiguous (for instance the much used and abused Grob-Prat classification, and later reproduced in Twiss *et al.*), or incomplete and simplistic (e.g. the Metcalfe classification, which fulfilled the objectives for which it was created, but is inadequate for evolutionary and paleoecological work).

Any new attempt to produce a standard classification of phytoliths should start by understanding where, and how their morphological features originate, and what is their natural variation and redundancy in different taxa, from empirical observations. At this point it is possible to accomplish this for grasses, and to some extent for sedges. This is the approach essayed in this section.

2.5.1 Grass blade and phytolith ontogeny

2.5.1.1 Ontogeny of the blades

Refer to Figure 5 for the following discussion.

All the aerial parts of grasses originate from the growing culm apex. This dome-shaped structure is formed by a corpus of undifferentiated cells covered by a two-layered tunica. The culm apex grows mainly by anticlinal division (i.e. by walls perpendicular to the surface). The ontogenesis of the typical grass leaf starts by the formation of ridges arising alternately around the culm apex, due to divisions of tunica cells by periclinal walls (i.e. parallel to the surface). These ridges grow to form leaf primordia with intercalary meristem at the base. Continuing transversal divisions of this intercalary meristem produce ultimately the cells which by differentiation will form the leaf (Barnard, 1964).

The details of this epigenetic chain of events, where each state conditions the transition probabilities (Note 1) towards the next, are as follows:

a) At intervals in the growing culm apex there is a certain probability that cells in the inner tunica layer (hypodermis or periphereal meristem) will divide by periclinal walls, instead of the anticlinal growth pattern. When this happens, it is the signal to start an epigenetic chain towards forming a leaf. Immediately, cells of the outer tunica layer (dermatogen or mantle)

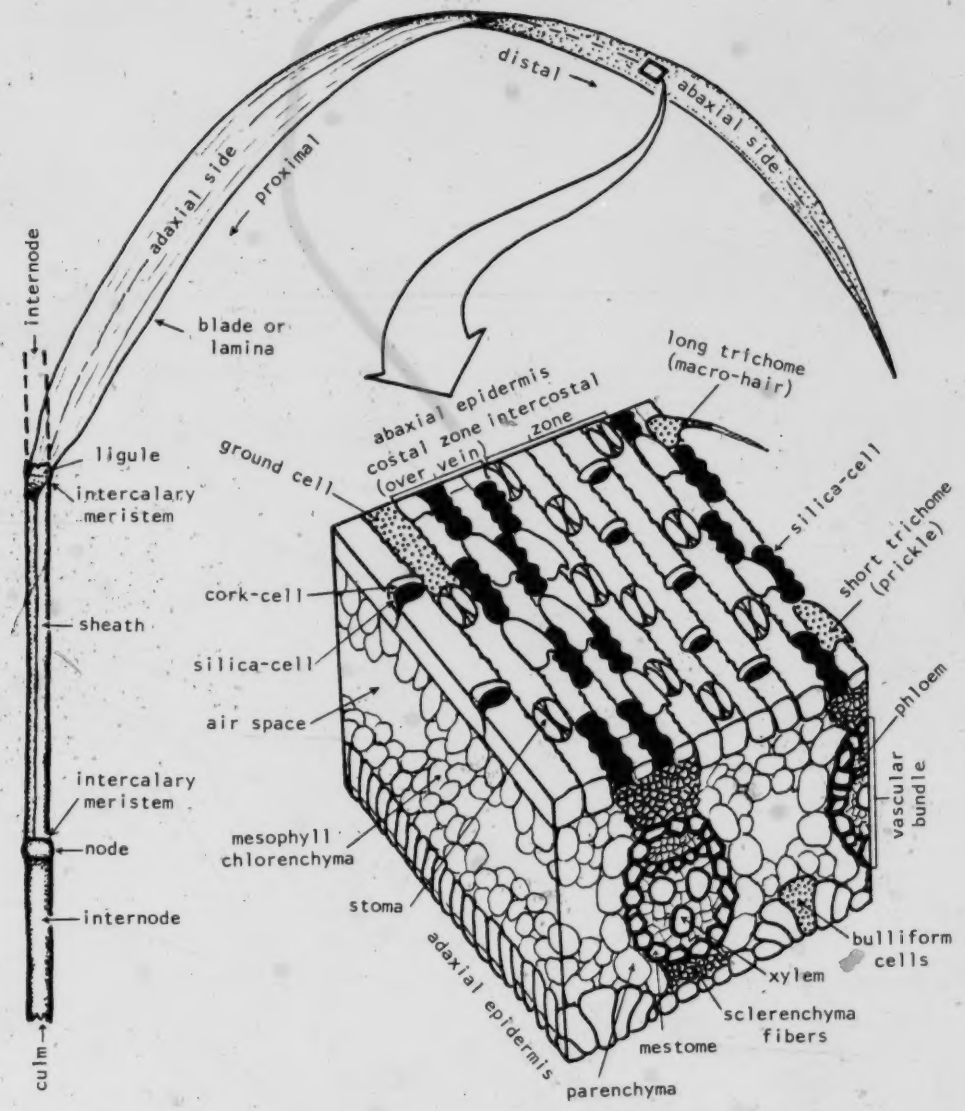


Figure 5 - Anatomy of a grass blade. Black cells contain t-phytoliths. Dotted cells contain c-phytoliths.

are induced to do the same.

b) As a response, cells of both tunica layers in the same horizontal plane half around the culm apex are triggered to periclinal divisions, forming a ridge, which is the beginning of the leaf primordium.

c) Initially the rate of transition to cellular division is higher in the mid-point of the ridge, causing the formation of a tip; later in ontogenesis the rate is equalized, and growth is parallel in all rows of cells, thus the shape of the grass blade.

d) The basal portion of the leaf primordia become the locus of cellular divisions forming a zone of intercalary meristem, from which leaf cells will differentiate.

e) The division of cells in this basal intercalary meristem is predominantly transverse, producing parallel rows of cells that lengthen the leaf primordium, until a transverse band of cells differentiates into compact parenchyma, dividing it into a proximal primordium and a distal primordium. Intercalary meristem at the base of the proximal primordium produces cells to form the sheath, while meristem at the base of the distal primordium (just above the parenchyma band) becomes the origin of blade cells. The ligule, when present, is formed by growth of adaxial cells at the level of the band.

f) Each row of cells produced by the intercalary meristem of the blade has a certain sequence of transition probabilities to differentiation. For example, to form the abaxial epidermis, certain rows could have only symmetrical divisions, while others could have different patterns of symmetrical and assymetric divisions. In the former case, the result could be rows of pure ground cells, or pure silica-cells (in this instance always costal). In the latter case, the result could be ground cells alternating with silica-cork cell pairs, silica cells, trichomes, or stomata. In the adaxial epidermis, cells of some rows could divide to produce exclusively bulliform cells. Also, the epidermal rows above the vascular bundles (costal zone) usually have different sets of transition probabilities than those of the intercostal zone.

Not only grass blades are formed by rows of cells with different combinations of transition probabilities to differentiation, but also the final morphology of differentiated cells is determined by a sequence of transition probabilities in epigenetic chains, ultimately controlled by genetic information, which is variable. Therefore, morphological variation in grass blades arises from variation in transition probabilities for the sequence of cells in rows, and for differentiation of each cell. Evolution of grass blades, as of any biological structure, occurs by alteration in

the values or numbers of these transition probabilities through genetic change. In fact, blades of grasses can be grouped in taxa with redundant combinations of differentiated rows and cells (e.g using the data of Metcalfe, 1960), which are correlated with taxa classified on the basis of other structures, such as reproductive organs. Therefore, blade anatomy reflects evolutionary relations.

2.5.1.2 Phytolith ontogeny

Kaufman *et al.* (1970, 1981), using light and TEM, provided the following data on ultrastructural cork-silica cell pair development in the internodal epidermis of *Avena*:

a) Cells of intercalary meristematic origin, which will form the epidermis (protoderm), divide assymetricaly in a row, producing alternating elongated and short cells. The elongated cells differentiate later into ground cells. The short cells divide again transversely producing two similar shorter cells.

b) The proximal of the short cells grows markedly (triplicating its size), and differentiates into a cork-cell, with heavily suberized walls, retaining its nucleus and organelles.

c) The distal one (silica-cell) also grows about three times or more in volume, but its nucleus, organelles, and membranes disintegrate. All that remains in the lumen are fibrillar elements and osmiophilic

droplets (which are stained with Sudan IV, being probably lipidic products of membrane and protoplasm disintegration). The differential growth of each cell of the short pair determines their shape, crescent for the cork-cell and oval for the silica-cell in epidermal view. It was also noticed that as a result of growth, the distal silica-cell protrudes from the surface of the epidermis.

d) The disorganized lumen of the silica-cell becomes filled with silica, by aggregation of biosilica spherules (which Kaufman *et al.* call "silica bodies") deposited in chains, in association with the fibrillar matrix. This completes the differentiation of the silica-cell.

To explain the sequential deposition of silica in the internodes, which starts at the top and progresses downwards, Kaufman *et al.* (1981) have proposed that silica is deposited as a result of ultrafiltration of polymers, formed when the conditions of silica concentration and pH are adequate. They called this process the "upside-down filter-cake model." The ideal conditions to start deposition would exist in the upper portions of the internode, immediately below the next node. So, moved by the transpiration stream, the xylem sap, which is carrying monosilicic acid in solution plus complex ions of silicon chelated by a tropolone derivative, finding the proper conditions above the

intercalary meristem zone (basal internode), would yield polymerized particles 10-30 Å in diameter, which in turn would be ultrafiltered by the tissues at the upper end of the internode. After the intercalary meristem activity ceases and its pH increases (probably by decrease in the level of endogenous gibberellins), it too becomes silicified. There are problems with this model, because it does not explain how high concentrations of monosilicic acid are rebuilt to silicify the next internode, after the sap lost silica by ultrafiltration; and because the heavier silicification occurs in epidermal cells, which are actually marginal to the sap stream. It also would fail to explain the same phenomenon in leaf epidermes.

Sangster and Parry (1981) have shown that silicification of root endodermal cells occurs as aggregates of biosilica spherules deposited centripetally, starting at the inner tangential wall. They also suggest that the small apolar $Si(OH)_4$ molecules, from the soil solution, could reach the root endodermis via the free-space or cell wall (apoplastic) pathway. Once the silicic acid molecules arrive to the suberized cells of the endodermis they are partially blocked, and tend to accumulate, until the concentration threshold for polymerization is reached and biosilica starts forming. However, these researchers observed abundant silica deposits in the endodermis of developing

aerial roots of sorghum, out of contact with soil or nutrient solution, which indicates that the reverse is also possible, that is silicic acid is able to leave the xylem and enter the endodermis from inside.

My original observations by light and SEM microscopy indicate that the epidermal cells of the grass blade silicify in three different ways: one always forming phytoliths in silica-cells, another forming phytoliths occasionally in any of the other cells, and finally by silicification of cell walls.

Silica-cells, paired with cork-cells or not (in the costal zone), initiate silicification at the outermost portions of the protruding external edges (Figure 6A) and continue centripetally until only the lipidic droplets remain unsilicified and trapped within the phytolith body (e.g. in the center of the corn phytolith in Figure 4B).

The initial silicification of the edges occurs by packing of very small biosilica polymers, directed by polar surfaces at the cell wall or fibrillar material accumulated against the cell wall. Still small silica spherules continue to accumulate against the external wall of the silica-cell probably oriented by fibrillar material (Figure 6C). Larger spherules (100-200 Å) are formed and continue to build the tertiary structure (Figure 6D), until the lumen is filled and the phytolith is completed. Under natural conditions silica cells

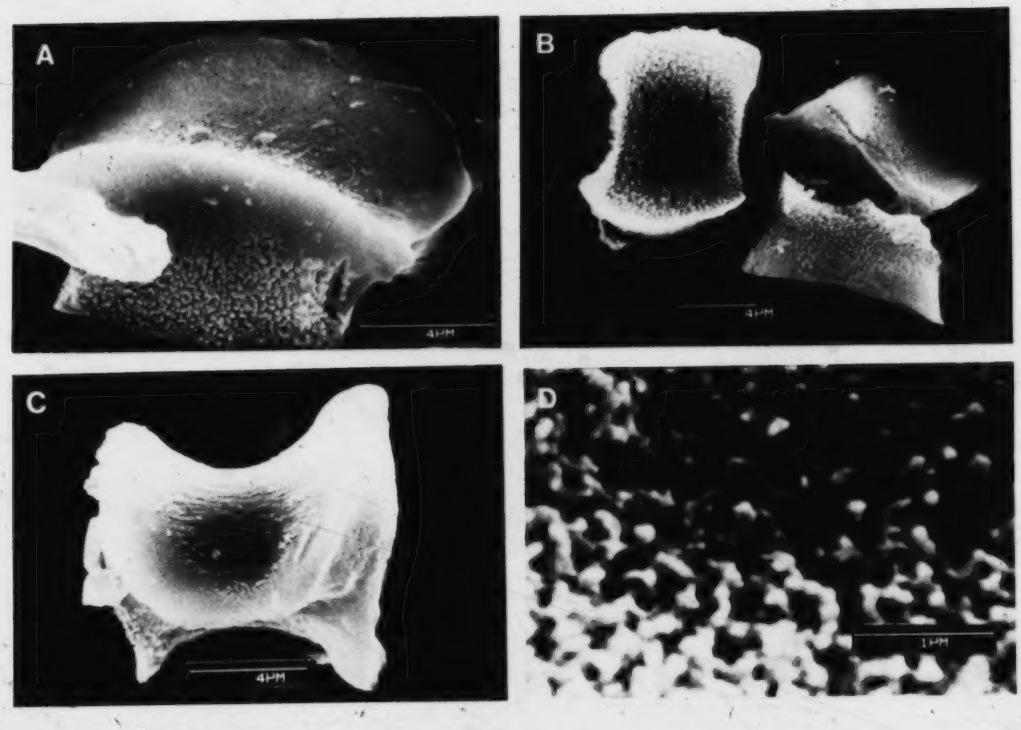


Figure 6 - Tertiary structure of biosilica in t-phytoliths of Bouteloua gracilis. A: selliform phytolith in lateral-oblique view, showing fine silicification at protruding edges and coarser silica spherules in the rest of the body. B: t-phytoliths in lower views. C: t-phytoliths in fron view, showing orientation of biosilica deposition along fibrils. D: detail of the tertiary structure, where the packing of spherules along chains is clear. Note the porous nature of phytolith biosilica.

always silicify, producing what I call **template-phytoliths.**

The other silicification process that forms phytoliths, can occur in any of the blade cells other than silica-cells. It starts by a very marked alteration, disorganization, or death of the cell, which basically only preserves the cell wall. Biosilica is simply precipitated within the walls of the cell until an internal cast of the cell is formed. Under natural conditions the formation of these phytoliths (which I call **cast-phytoliths**) is generally random, but some cells such as the trichomes generally produce phytoliths, particularly if evapotranspiration is intense.

The two kinds of phytoliths can be recognized, even if isolated from the blade, by transmitted light microscopy. The template-phytoliths (or t-phytoliths), derived from silica-cells, have a very transparent and clear structure, and also contain vacuoles corresponding to the lipidic droplets. While the other cell phytoliths (cast or c-phytoliths), have a more granular (microscopically opaque or darker) structure, and do not have the vacuoles (although imperfect silicification or corrosion can sometimes be misleading).

From the above and additional original research observations, it is possible at this point to propose the following summarized model for phytolith formation

in the grass blade:

a) The intercalary meristem distal to the sheath-blade parenchymatous interface produces rows of cells, which have different transition probabilities of division and differentiation along the ontogenic epigenetic chains. These transition probabilities are controlled by the contextual reference system and the previous state. Two general kinds of cells are produced, namely silica-cells and all the others. The former always yield template-phytoliths, whereas the latter, if eventually silicified internally, produce cast-phytoliths.

b) Ontogenesis of t-phytoliths:

In the meristematic row that will produce ground cells (also called "long" or "fundamental" cells), and pairs of cork and silica-cells (usually in the intercostal zone), transversal assymetric divisions occur at intervals. The shorter cells divide transversely again, but now symmetrically. Of these, the proximal cell will differentiate into a cork cell, while the distal one will become a silica-cell.

The differentiation of the cork-cell involves: growth to about three times the original volume (usually partially embracing the distal cell), and suberization of the walls, but not loss of the nucleus and organelles.

The differentiation of the distal cell into a silica-cell starts by growth even more accentuated than the cork-cell. The cell external surface protrudes, and generally the edges extrude more prominently. This "overflow" of the cell is perhaps determined by the space available to growth being limited by the surrounding cells. Then, it looses the nucleus, membranes, and all the organelles, becoming filled with fibrillar material, and some lipidic droplets (mainly from membrane disintegration). It seems that the cell becomes even more turgid once the process of internal disorganization starts, perhaps due to osmosis when the cell membrane barrier is altered. Because of this alteration of the cellular membrane, it is hypothesized here that a process of reverse osmosis or ultrafiltration starts at the surface of the cell, which begins "leaking" water to the outside where it is evaporated. Supporting evidence for this unidirectional flux is provided by the data of Bombin and Muhelenbachs (1980), which indicates formation of phytolith biosilica in isotopic equilibrium with internal water. The conditions inside the cell now favor the polymerization of monosilicic acid, initially into very small biosilica spherules. The spherules are directed by the outward flux towards the internal surface of the external wall, preferentially to the extruded edges (which seem to be thinner and perhaps more permeable to water), where the

spherules are packed into a relatively compact tertiary structure. The interactions of the polar surfaces of the spherules, the fibrillar cytoplasm, and the cell wall, act as guides for selformation of the tertiary structure. After the initial deposition of small spherules, the intercellular conditions become favorable to further development of the secondary structure of biosilica polymers, and larger spherules are generated, which continue to pack centripetally, until the t-phytolith is completed. The lipidic droplets, being internally apolar are not silicified, resulting in their segregation, which will constitute the typical vacuoles of silica-cell phytoliths.

The same general process above (for silica-cells in cork-silica cell pairs) takes place in the formation of phytoliths within single silica-cells located in the costal zones. For example, all the elongated silica-cells in the Pooideae, which always occur in this anatomical position.

The general outline of phytoliths is determined by the shape of the mother-cell, which is also in turn affected by the differential growth and shape of the neighbouring cells. In the case of silica-cells, which grow beyond the confines of the space provided by the surrounding cells, forcing them to protrude externally (Figure 4C), the mode of extrusion is also a factor in the final morphology of t-phytoliths, particularly of

the external surface, because it is not identical in all phytoliths. This extrusion is in general more accentuated around the edges of the external surface, so most silica-cell derived phytoliths will have a concave upper surface. The protruding edge can be more or less smooth, or be interrupted by different kinds of constrictions, due to differential resistance to expansion (e.g. by cell wall bonding). Therefore, the final morphology of the edge depends on properties of the cell wall, which is ultimately genetically controlled (and thus subjected to evolutionary change). Other structures that are reproduced in the surface of phytoliths are cell wall pits , and intercellular spaces, for example, when there are two fiber cells below a silica cell that partially intrudes the space between them, a keel is formed on the lower surface of the phytolith.

c) Ontogenesis of c-phytoliths:

Internal silicification can occur eventually in any of the other cells of the grass blade epidermis, namely: ground cells, trichomes, bulliforms, and stomata; and very rarely in cells of the mid-portion of the blade, namely: mesophyll chlorenchyma, parenchyma, mestome, sclerenchyma, and vascular elements. The c-phytoliths formed within any of these cells are simply more or less perfect internal casts, and occur when cells die or are functionally very altered. The same mechanism of reverse

osmosis or ultrafiltration could apply here, without the template effect of the fibrillar matrix described for the silica-cells.

The third kind of silicification that occurs in blade cells (generally epidermal) is by siliceous impregnation of the cell wall. This happens generally when there is a strong gradient between internal water supply and evapotranspiration, for example in semi-aquatic or marsh grasses with emergent blades, or irrigated plants in dry climates. In this case, perhaps outward apoplastic pathways of sap silicic acid play a role. The same steep gradient conditions also favor the formation of phytoliths, and intercellular silicic concretions.

2.5.2 Morphological information in grass phytoliths

The first step in identifying the redundancy of phytoliths and their Linnean taxa correlates is to identify the most significant morphological loci of encoded information. Exclusive use of generalized and vague descriptions such as "hats", "dumbbells", "saddles", or "elongates" are not adequate for phytolith analysis, because they are very redundant throughout the grasses. A "dumbbell", for example, can occur in members of any of the grass subfamilies (Metcalfe, 1960; Gould and Shaw, 1983). The aim is to find singular redundancies instead.

The system being proposed here starts by decoding information to segregate the phytoliths in two groups: t-phytoliths (i.e. from silica-cells), and c-phytoliths (i.e. from any other cell). In reference samples this is straightforward. In fossil samples, t-phytoliths can be recognized because they are more transparent; have vacuoles; are usually patelliform (knee-cap shaped) with or without keel, cymbiform (boat-shaped) with or without keel, or selliform (saddle-shaped); and do not have any of the c-phytolith attributes. On the other hand, c-phytoliths are usually only transluscent, granular ("darker" under the light microscope), do not have true vacuoles, and display the characteristic morphology of their mother-cells. The only possible ambiguity might arise, occasionally, in differentiating elongated corroded t-phytoliths from ground cell c-phytoliths (these usually have more irregular surface and outline). If this happens, it is safer to identify them as cf. c-phytoliths (because these have a more generalized distribution), or even better as *incertae sedis*. Another clue is that large (>60 micrometers) elongated phytoliths are usually c-phytoliths. This distinction between elongated phytoliths is important, because elongated t-phytoliths are exclusive of the subfamily Pooideae.

The next step is to translate the information contained in the different parts of the phytoliths, which is more effectively done by systematic analysis of their structure in three orthogonal views (upper, lateral, and frontal

views), as indicated in Figure 7. In light microscopy, if the mounting medium is too viscous or rigid, or the preparation is a leaf epidermis specimen, this is not possible. In this case, the information obtained has to be maximized by inference (e.g. through focus tomography), trying to model the tridimensional structures as closely as possible. In analyzing c-phytoliths usually one view provides sufficient information for analysis. The following views are recommended for c-phytoliths of different cells:

trichomes - lateral view;

ground cells - upper view;

stomata - upper view;

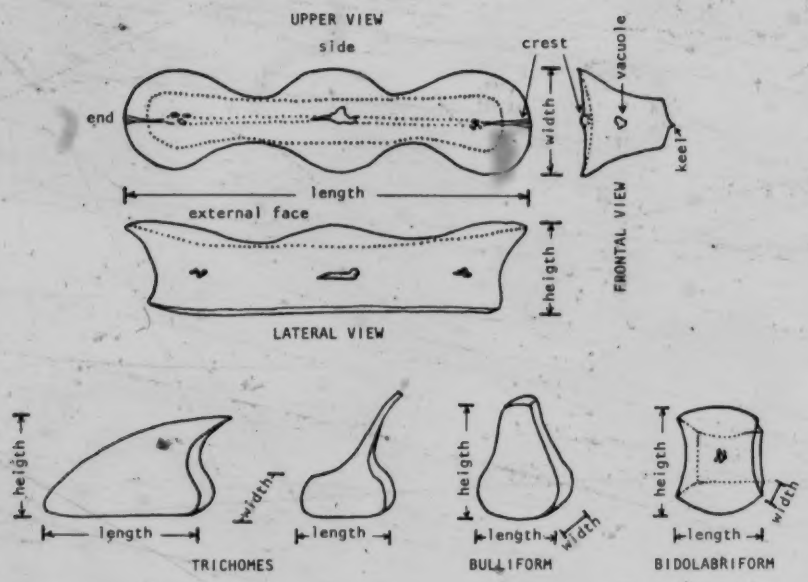
xylem - lateral or upper views;

fibers - lateral or upper views; and

bulliforms - frontal view.

As suggested by Metcalfe (1960), the standard orientation of the blade for analysis, and reference, is with the longitudinal rows of epidermal cells horizontal to the microscopist.

The most common shapes of grass phytoliths in the three views are listed and illustrated in Figure 8. The three basic tridimensional shapes of t-phytoliths, namely, patelliform, cymbiform and selliform, are also represented in Figure 8. The morphology of sides and ends normally encountered in non-isodiametric phytoliths are represented in Figure 7.



MORPHOLOGY OF SIDES
(outside up)

- smooth
- ondulate shallow
- ondulate deep
- sinuate deep
- sinuate shallow
- angulo-sinuate
- acutangulo-sinuate
- sinuate-ondulate
- crenate
- dentate
- serrate
- spiny
- spiny-pileate
- irregular

MORPHOLOGY OF ENDS

upper view:

- straight
- convex
- mamillate
- concave
- notched
- beveled
- pointed

lateral view:

- straight
- up-beveled
- down-beveled
- concave
- concave up-beveled
- concave down-beveled
- convex up-beveled
- convex down-beveled

processes:

- spikes
- basal protuberances

Figure 7 - Orientation, measurement, and morphology of grass phytoliths I.

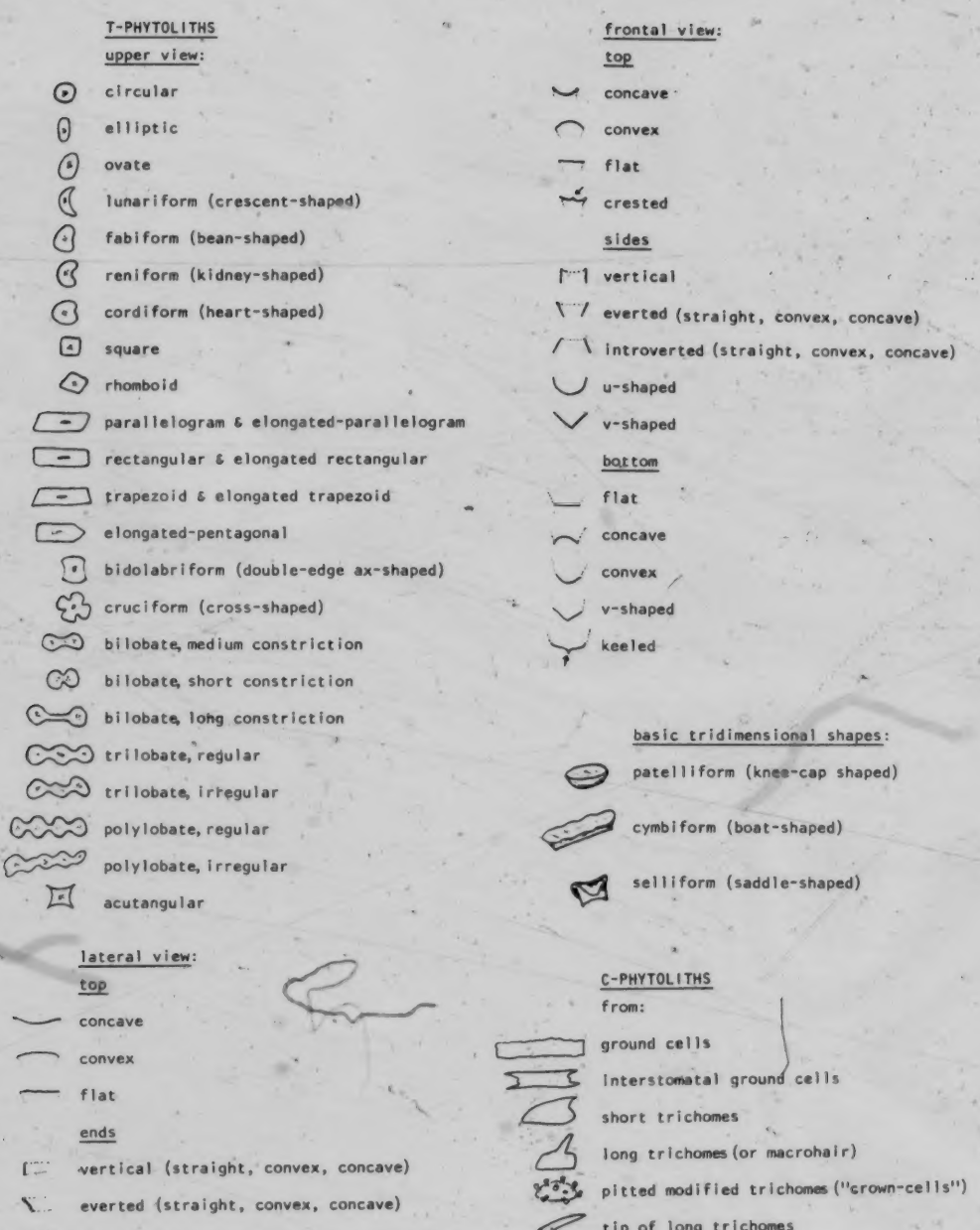


Figure 8 - Morphology of grass phytoliths II.

Other parameters that should be recorded when indicated are, the presence of crests, keel, vacuoles, and staining. Information about preservation, other occurrences, and bibliographic references are also useful. A scaled sketch showing the three views (and photographs if possible), should accompany descriptions of morphotypes. Any details revealed by SEM should be described. A model of a protocol sheet for phytolith description, which can be adapted for computerization, is reproduced in Note 3.

When all the information suggested above is decoded from phytoliths (particularly t-phytoliths), and arranged hierarchically, a remarkable degree of discrimination of Linnean taxa can be attained, in some cases (e.g. maize) even at the species level. Modern balanced grass classifications show higher correlation with phytolith morphotypes, which indicates that some of the past confusions in discrimination of grasses based on phytoliths were due to inadequate Linnean classifications of the Poaceae. The taxonomy and nomenclature of grass subfamilies, tribes, and genera followed here, is that of Gould & Shaw (1983).

I suggest that a classification system, or key, of any phytolith set, should use the redundancy of parametric and non-parametric morphological attributes to cluster the phytoliths, initially by anatomical origin, and then hierarchically, until only idiosyncratic information remains. The identification of Quaternary fossil phytoliths

is done by comparison of morphological attibutes with known phytoliths, which makes it analogous to already established methods of palynomorph analysis (e.g. pollen-spores and diatoms).

The limiting factor for precision in identification of fossil phytoliths is the representativeness of the available reference collection. The desirable or necessary Linnean taxonomic level of discrimination depends on the kind of question being asked, or hypothesis being tested. Identification at the level of tribe, or in some cases genus, is sufficient in many situations, for example in the application presented in chapter 3. Sometimes even the sole phytolith morphotype diversity or abundance is a very key piece of information in paleoecological research. In archaeological studies, when cultivated plants are searched through phytolith analysis, detail, precision, and specificity are required to discriminate the crops.

Figures 9 through 17 further illustrate morphological variation in grass phytoliths, and the use of the nomenclature and classification introduced above.

Recently I have started the study of geometric information coded on phytoliths. This approach is still tentative, but it already revealed an exciting and potentially powerful insight into the study of natural forms. In my first attempt to model phytoliths geometrically, I tried to fit surfaces to the three basic t-phytolith tridimensional shapes, and found that quadric

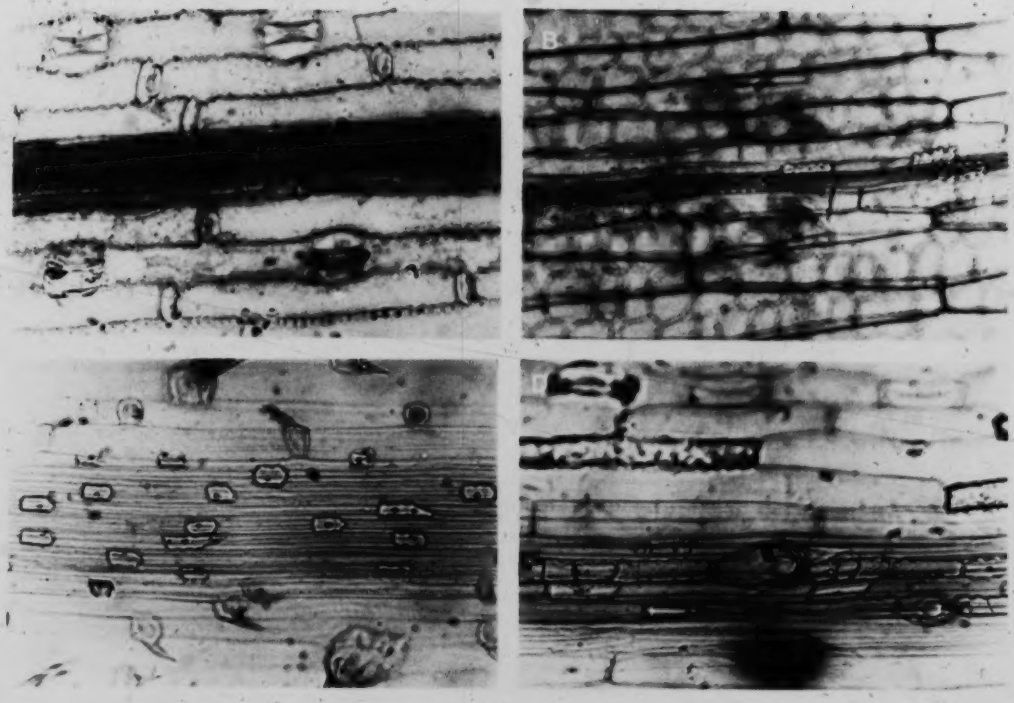


Figure 9 - Phytoliths in epidermal preparations.
A: Elymus canadensis (Pooideae, Triticeae), costal and intercostal t-phytoliths patelliform, elliptic to ovate to fabiform.
B: Poa annua (Pooideae, Poeae), costal t-phytoliths cymbiform, rectangular to parallelogram, shallow sinuate to crenate.
C: Koeleria gracilis (Pooideae, Aveneae), costal t-phytoliths cymbiform, rectangular to trapezoid to low pentagonal, shallow angulo-sinuate to sinuate ondulate, keeled (see Fig. 15B); intercostal trichomes with silicified tips. D: Hordeum vulgare (Pooideae, Triticeae), costal t-phytoliths cymbiform, rectangular to parallelogram to trapezoid, ondulate to shallow sinuate; intercostal ground cell c-phytoliths. Note differences between t-phytoliths and c-phytoliths ("granular"), variation among the Pooideae, and fractured phytoliths in 10D. Scale: each photo covers 200 x 300 µm.

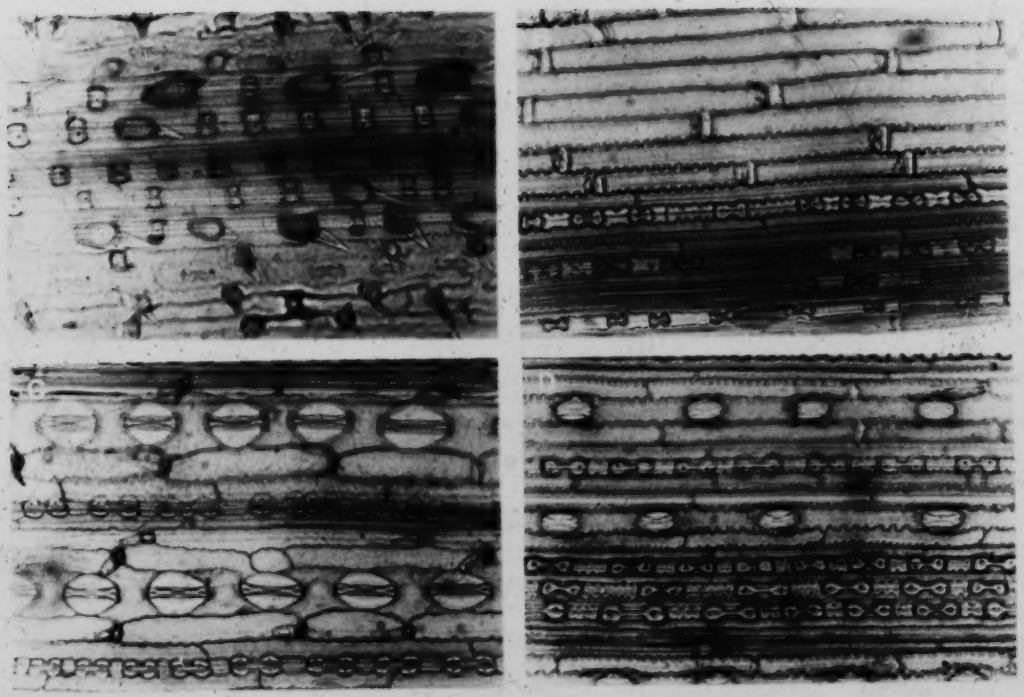


Figure 10 - Phytoliths in epidermal preparations.
A: Bouteloa curtipendula (Chloridoideae, Chlorideae), costal t-phytoliths selliform, keeled transversally. B: Danthonia spicata (Arundinoideae, Danthonieae), intercostal t-phytoliths patelliform, reniform to bilobate; costal t-phytoliths bilobate medium to short constriction; costal t-phytoliths trilobate irregular.
C: Andropogon shrivensis (Panicoideae, Andropogoneae), costal t-phytoliths bilobate medium to long constriction; costal t-phytoliths trilobate irregular; trichomes with silicified bases. Note markedly different focal planes of bilobates and trilobates, which is typical of the Andropogoneae. D: Aristida setacea (Chloridoideae, Aristideae) costal t-phytoliths bilobate generally long constriction. Scale: each photo covers 200 x 300 um.

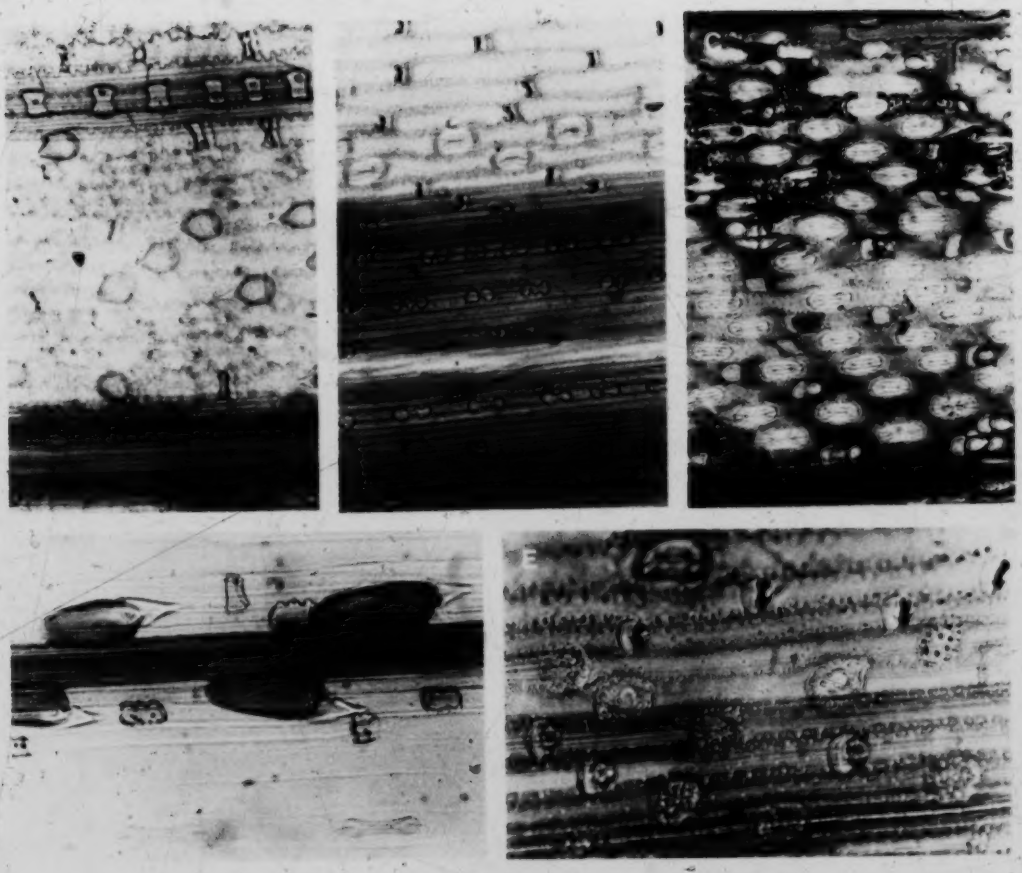


Figure 11 - Phytoliths in epidermal preparations.
A: Bambusa vulgaris (Bambusoideae, Bambuseae), costal t-phytoliths selliform, large bidolabriform; intercostal t-phytoliths selliform, very narrow bidolabriform; tip of trichomes silicified.
B: Stipa dregeana (Pooideae, Stipeae), costal t-phytoliths bilobate short to medium constriction irregular; costal t-phytoliths trilobate irregular; intercostal t-phytoliths patelliform, elliptic to ovate to fabiform. C: Phragmites australis (Arundinoideae, Arundineae), costal t-phytoliths selliform (bidolabriform with markedly different focal planes); costal short trichome c-phytoliths (right corner); intercostal t-phytoliths patelliform, circular to elliptic to ovate; intercostal interstomatal ground cell c-phytoliths.
D: Bromus carinatus (Pooideae, Poeae, section Ceratochloa), pericostal t-phytoliths cymbiform, rectangular to square to trapezoid (some very narrow), sinuate; pericostal short trichomes with tips silicified.
E: Triticum aestivum (Pooideae, Triticeae), costal pitted modified short trichome ("crown-cell") spiny-pileate c-phytoliths (see 16C); intercostal and costal t-phytoliths patelliform, circular to elliptic.
Scale: each photo covers 200 x 300 µm.

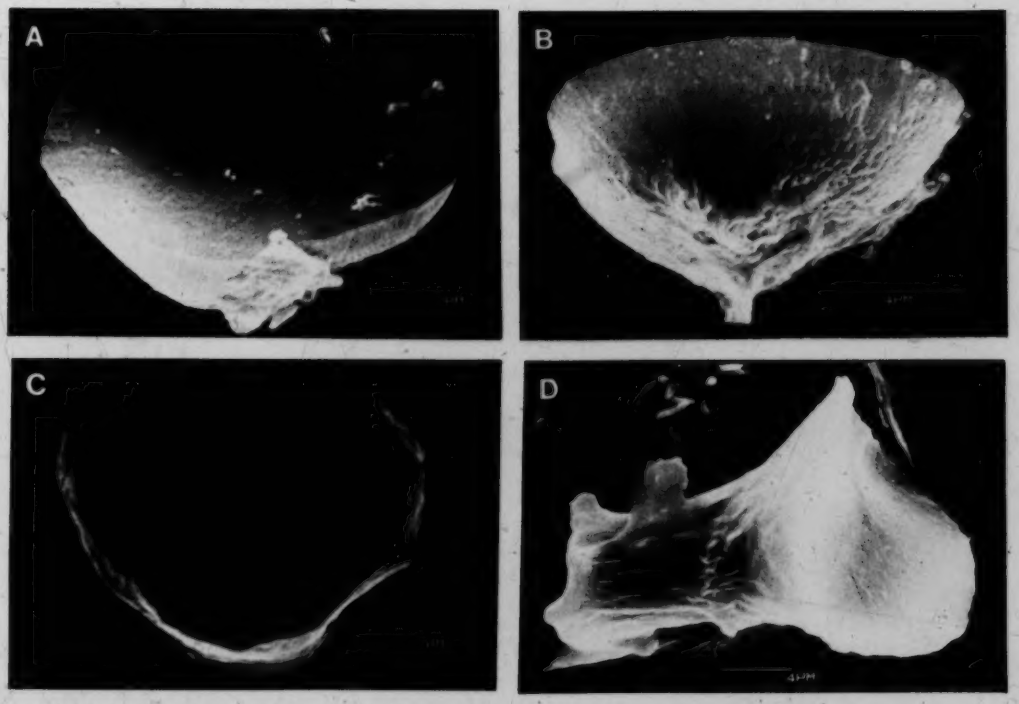


Figure 12 - Phytoliths in SEM. A and B: Festuca ovina (Pooideae, Poeae), costal/intercostal t-phytoliths patelliform, circular, keeled. A, upper oblique view; B, frontal oblique view. C: Poa alpigena (Pooideae, Poeae), intercostal t-phytolith patelliform, reniform. D: Arctophila fulva (Pooideae, Poeae), costal (?) t-phytolith cymbiform, elliptical, very tall.

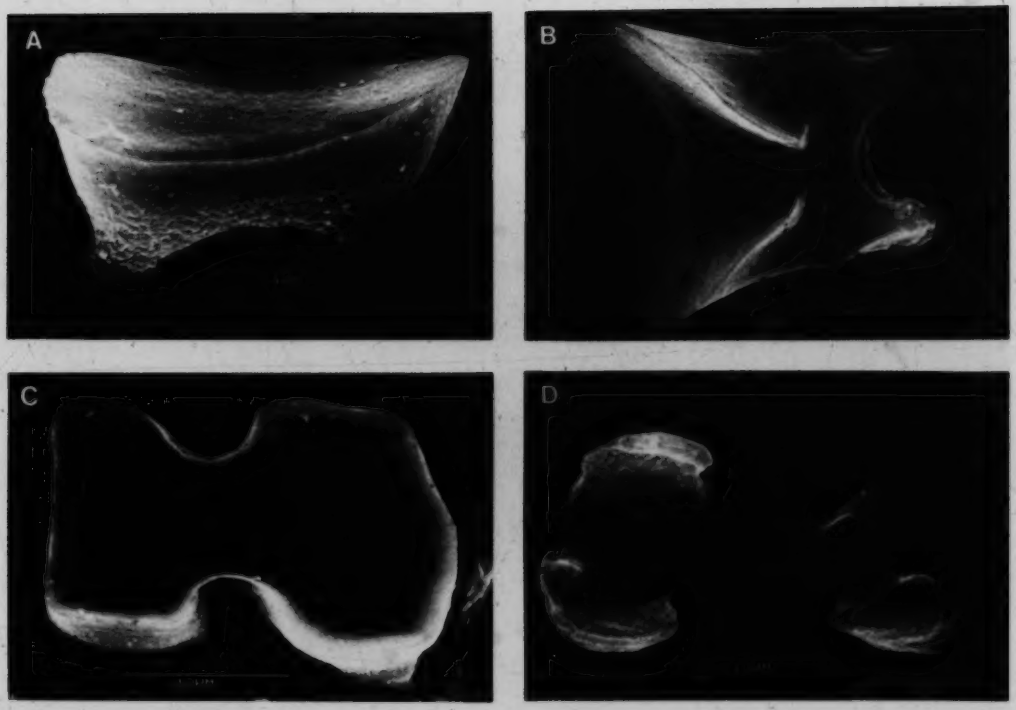


Figure 13 - Phytoliths in SEM. A: Stipa richardsonii (Pooideae, Stipeae), intercostal t-phytolith patelliform, elliptic, marked basal protuberances. Note fine tertiary biosilica structure at the edges and coarser at the base. B: Spartina gracilis (Chloridoideae, Chloridae), costal t-phytolith patelliform tall. C: Orizopsis hymenoides (Pooideae, Stipeae), costal t-phytolith bilobate, short constrictions, straight ends. D: Schizachyrium scoparium (Panicoideae, Andropodoneae), costal t-phytolith bilobate, long constriction, lobes bent upwards (responsible for difference in focal plane).

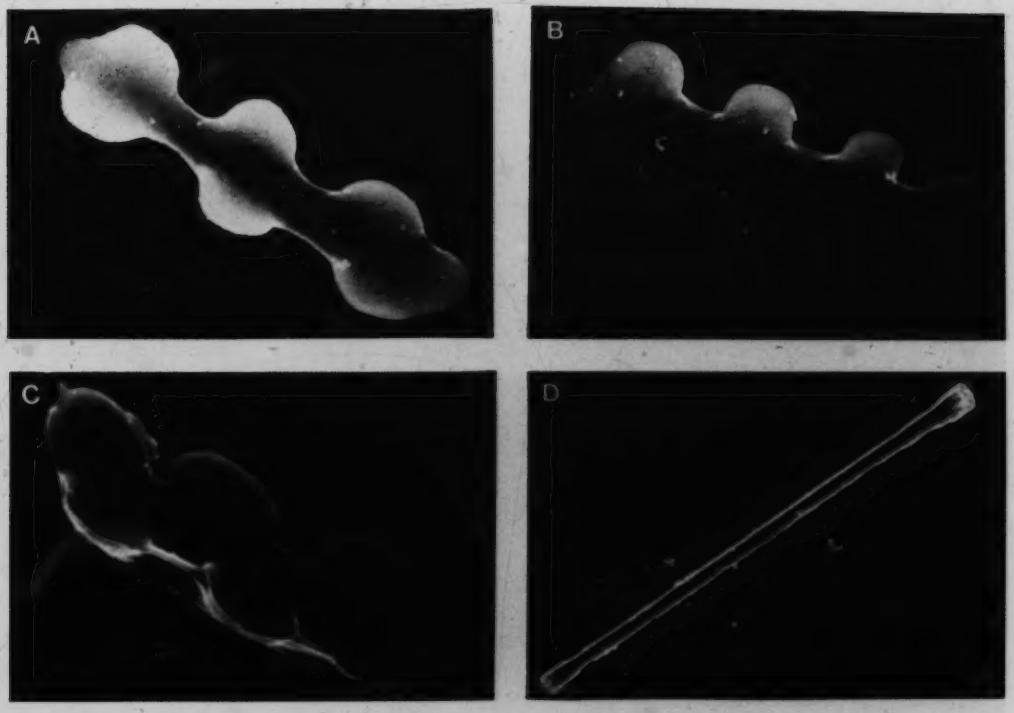


Figure 14 - Phytoliths in SEM. A: Glyceria pauciflora (Pooideae, Meliceae), costal t-phytolith trilobate regular, end mamillate. B: Pleuropogon sabinii (Pooideae, Meliceae), costal t-phytolith cymbiform, trapezoid, sinuate deep (slightly angulo-sinuate), ends low mamillate. C: Glyceria pauciflora (Pooideae, Meliceae), costal t-phytolith trilobate regular, end wide mamillate, end with spike. D: Agrostis borealis (Pooideae, Avenease), costal t-phytolith cymbiform, rectangular extremely elongated, smooth, ends spatulated with crest.

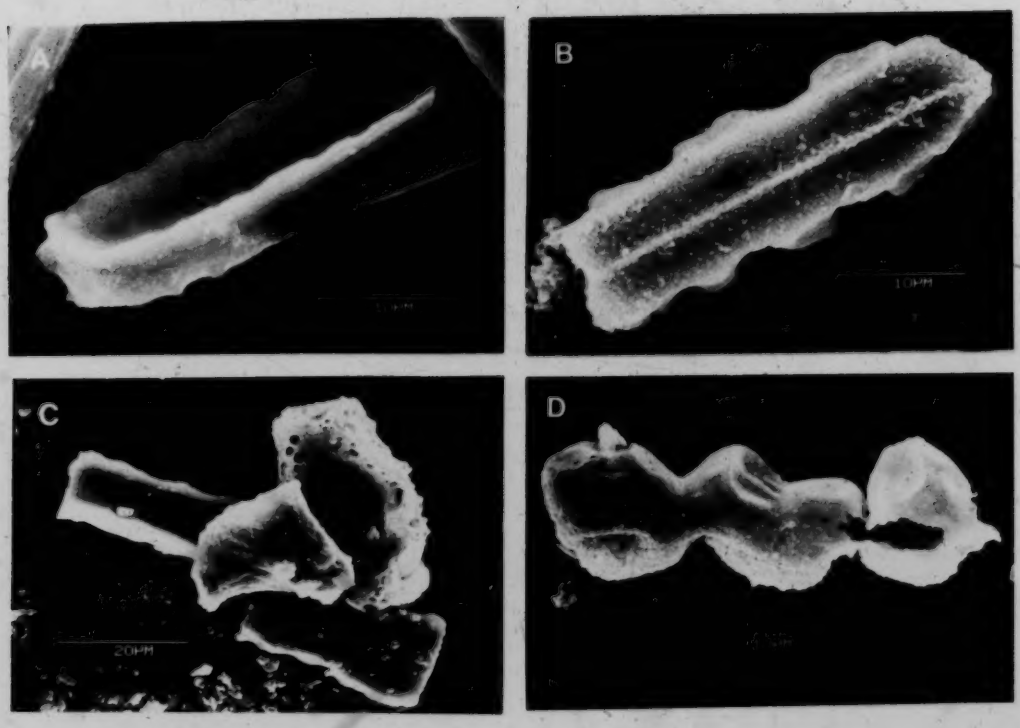


Figure 15 - Phytoliths in SEM. A: Bromus ciliatus (Pooideae, Poeae, section Pnigma), costal t-phytolith cymbiform, rectangular, ondulate shallow, ends convex. B: Koeleria gracilis (Pooidea, Aveneae), costal t-phytolith cymbiform, elongated-pentagonal, shallow sinuate-ondulate, keeled. C: Agropyron cristatum (Pooideae, Triticeae), group of four phytoliths, the center one is a bulliform cell c-phytolith. D: Agropyron cristatum (Pooideae, Triticeae), mesophyll cell c-phytolith.

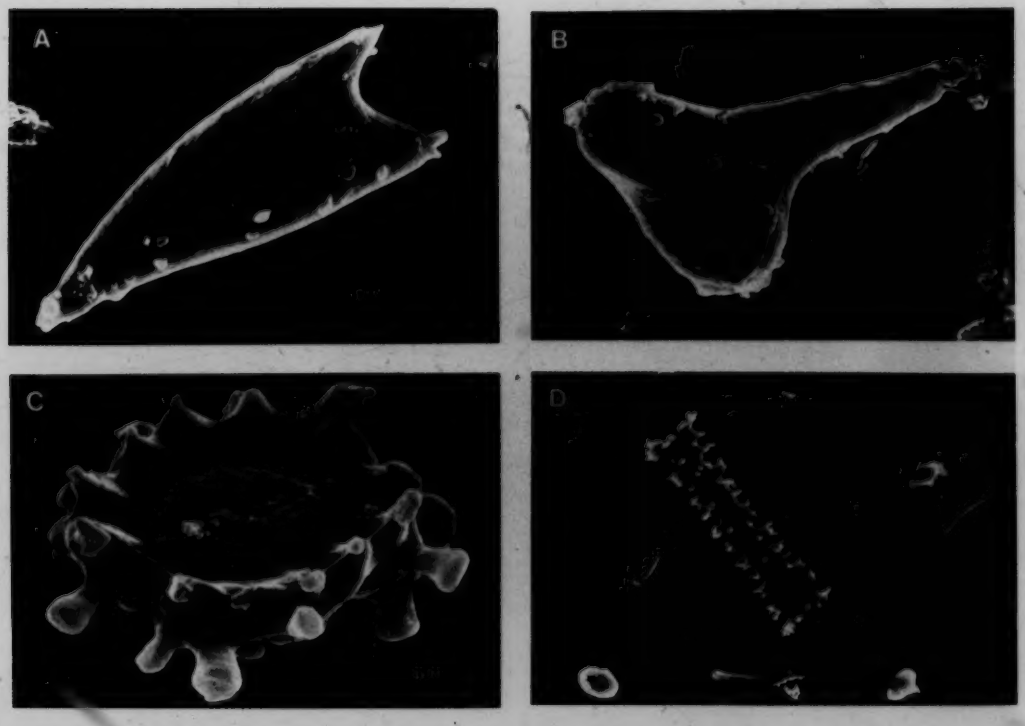


Figure 16 - Phytoliths in SEM. A: Agrostis scabra (Pooideae, Aveneae), short trichome c-phytolith. B: Agrostis scabra (Pooideae, Aveneae), long trichome (macrohair) c-phytolith. C: Agropyron smithii (Pooideae, Triticeae), costal spiny-pileate c-phytolith from a pitted modified short trichome ("crown cell"). These are characteristic of the Triticeae. D: Agropyron smithii (Pooideae, Triticeae), intercostal spiny-pileate c-phytolith from a pitted ground cell.

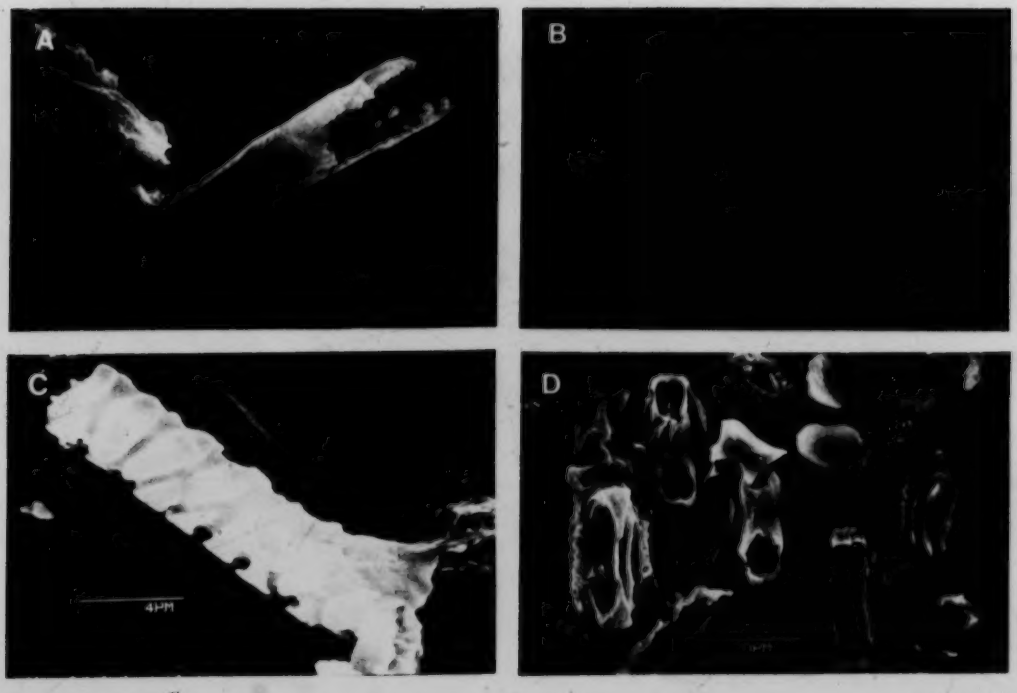


Figure 17 - Phytoliths in SEM. A: Poa glauca (Pooideae, Poeae), tip of long trichome c-phytolith. B: Muhlenbergia richardsonis (Chloridoideae, Eragrosteae), intercostal interstomatal ground cell c-phytolith. C: Puccinellia arctica (Pooideae, Poeae), xylem c-phytolith. D: Phragmites communis (Arundinoideae, Arundineae), heavily silicified epidermis, including stomata c-phytoliths. Free on surface of preparation, there are four t-phytoliths patelliform, fabiform, with basal protuberances.

surfaces approximate quite well the natural ones. The patelliform surfaces conform to paraboloid ($x^2/a^2 + y^2/b^2 = z/c$), or half hyperboloid of two sheets ($x^2/a^2 + y^2/b^2 - z^2/c^2 = -1$) surfaces. The cymbiform surfaces are deformed versions of the hyperboloid of one sheet surface ($x^2/a^2 + y^2/b^2 - z^2/c^2 = 1$). An interesting consequence is that an evolutionary model of these three phytolith shapes would suggest that:

a) Being hyperboloid, patelliform and cymbiform phytoliths are evolutionarily related, their morphological difference resulting from a topological jump, which can be modeled by a change in sign on the terms of their respective equations.

b) Selliform phytoliths are not directly related to the two other forms referred above, but are to the paraboloid patelliforms, their difference being also the result of a topological jump, modeled by a change in sign in one term of their respective equations.

The next attempt to model phytoliths geometrically, was trying to fit plane and higher plane curves to the shapes of the upper surfaces of t-phytoliths. Here also, good approximations were obtained in the studied cases. The simplest matches are obtained with the upper surfaces of circular, elliptic, and ovate patelliforms. So far, the cycloids seem to have the most general application. For example, the epicycloids (curves described by a point on the circumference of a circle as it rolls around another

circle), which are described by the equations

$$x = (a + b)\cos\phi - b\cos[(a + b)\phi/b], \text{ and}$$

$$y = (a + b)\sin\phi - b\sin[(a + b)\phi/b],$$

where a and b are respectively the radii of the fixed and moving circles, and ϕ is the angle described by the moving circle in relation to the origin of the coordinates, and the point of departure of the moving circle. If $a = nb$ the curve is an n-cusped epicycloid. The cardioid (one-cusped epicycloid) fits well patelliforms with fabiform, reniform, and cordiform upper surfaces. The nephroid (two-cusped epicycloid) conforms to bilobates. The four-cusped epicycloid matches the cruciforms (in the case of maize, sometimes there are even "defective" cruciform phytoliths that match the three-cusped epicycloid).

Trilobates, polylobates, and a variety of cymbiforms with curvilinear edges, are fitted best by epicycloids produced by a circle moving around an ellongated ellipse. Acutangular phytoliths correspond to the astroid (four-cusped hypocycloid described by a point on the circumference of a circle moving around the inside of another circle).

On this subject of plane curves, there are also interesting consequential predictions for evolutionary modeling of phytolith morphological changes. For example, the evolutionary relation between monoconstricted patelliforms, bilobates, trilobates, and polylobates would be through topological transformations modeled by changes in

the proportions between the radii a and b.

On a more speculative line of thinking, based upon these geometric studies, it seems plausible to hypothesize that the phytolith evidence indicate an arundinoid-like ancestor for the grasses. This would then split into Arundineae and Danthonieae lines, which would respectively evolve into grasses classified today as Arundineae, Oryzoideae, Bambusoideae, and Chloridoideae on one side, and Danthonieae, Panicoideae, and Pooideae on the other. Evidently, this has to be tested by studying the fossil record in Cretaceous and Tertiary deposits, which is a project that I am just starting to work on.

2.5.3 Sedge phytoliths

Phytoliths from the Cyperaceae have been studied less than those from the Poaceae. Although general, Metcalfe (1971) still is the most comprehensive reference on sedge phytoliths. They seem to hold a potential similar to that of the grasses for evolutionary and paleoecological studies. From my own light and SEM microscopic observations, as in the grasses, I propose the existence of two kinds of phytoliths in sedges: t-phytoliths (from silica-cells), and c-phytoliths (from any other cell). In all the species studied, t-phytoliths are exclusively present in the costal zone (e.g. Figures 18A and 18B).

The basic tridimensional shape of sedge t-phytoliths is scutiform (buckler or shield-shaped) umbonate (with a

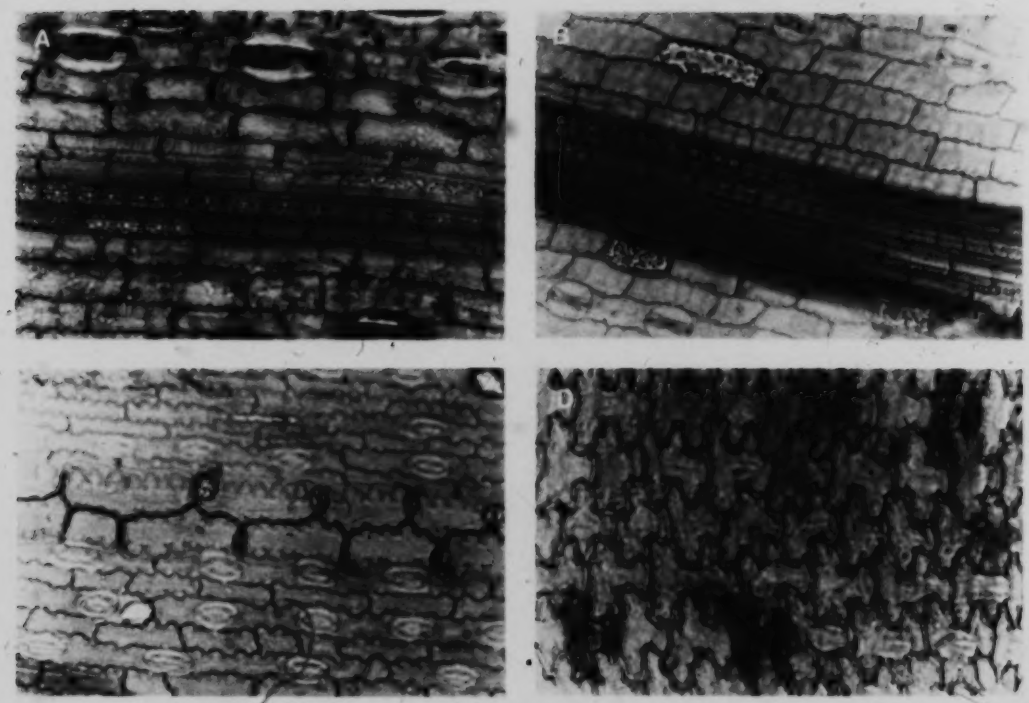


Figure 18 - Sedge phytoliths in epidermal preparations.
A: Eriphorum latifolium, scutiform phytoliths, pointed protuberance, four to eight tubercles regularly distributed around the periphery. B: Kobresia royleana, scutiform phytoliths, protuberance rounded to unconspicuous, tubercles variable irregularly distributed and very conspicuous; ground cell phytoliths tabular, rectangular to trapeziform, spiny sides. C: Scleria banbariensis, hemispherical phytoliths on tranversal walls of costal cells, echinulate to verrucate. D: Mapania wallichii, ground cell c-phytoliths of shape peculiar to the genus Mapania. Scale: each photo covers 200 x 300 µm.

central boss or protuberance), as those illustrated in Figures 19A, 19C, and 19D. In addition, many scutiform phytoliths also have small tubercles on the upper surface. Their morphology, number, and position is variable; in some taxa the tubercles are located around the protuberance ("satellites"), as shown in Figures 18A, 18B, and 19C; in others, they are polarized, as in the phytolith of Figure 20C; yet in others, the tubercles are distributed over the protuberance (Figures 19D, and 20D), or the whole surface of the phytolith (Figure 18B). In some sedges (e.g. *Scirpus*) these tubercles are cochleate (coiled like a snail shell), and cover most of the upper surface of the scutiforms (Figure 20B). The scutiforms occur one per cell, two per cell fused (Figure 20D) or not, and, more rarely, several per cell.

The scutiform t-phytoliths from sedges are essentially very different from grass t-phytoliths, which indicates (as do other anatomical features) a very considerable evolutionary distance between the plants grouped within the Poaceae and the Cyperaceae. If anything, the sedge phytoliths are perhaps morphologically closer to the ones from Palmae (Tomlinson, 1961).

The ontogeny of scutiform t-phytoliths needs further investigation. My preliminary observations indicate that they always form at the base of the epidermal cells, and that the cellular material on top of them serves as the template to start silicification, and produce the upper

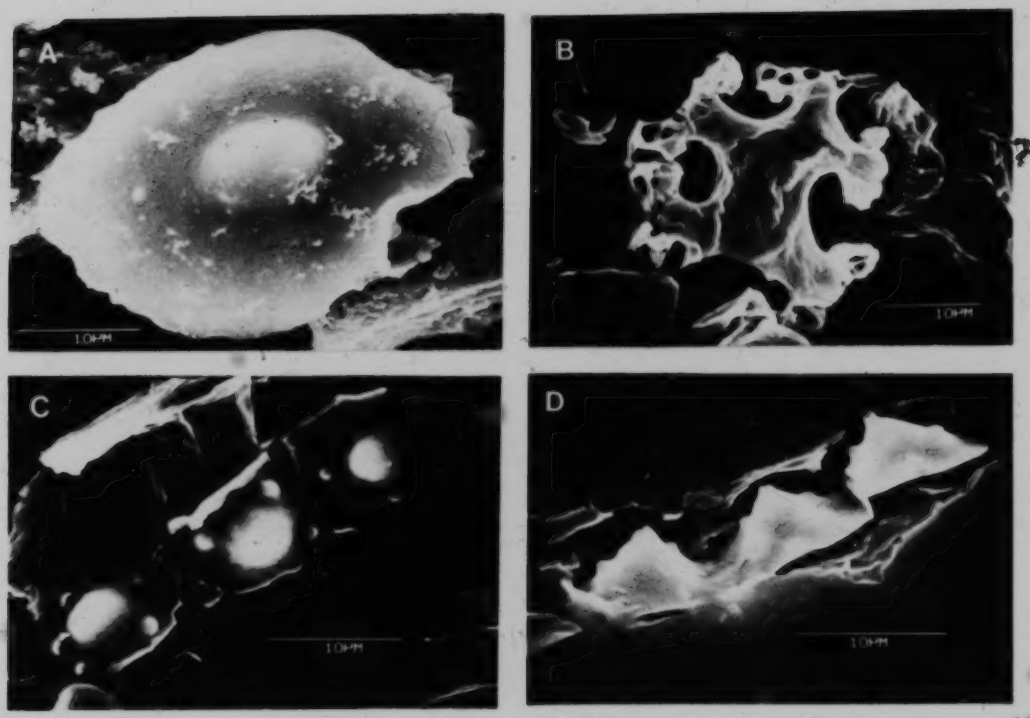


Figure 19 - Sedge phytoliths in SEM. A: Carex stenophylla, **scutiform phytolith, protuberance of medium size rounded, no tubercles. B:** Eleocharis palustris, **stellate mesophyll cell phytolith. C:** Eleocharis palustris, **scutiform phytoliths, protuberance large and rounded, tubercles 3 to 6 around the protuberance. D:** Eriophorum angustifolium, scutiform phytoliths, protuberance very large and pointed, tubercles generaly 4 or 5 on the protuberance.

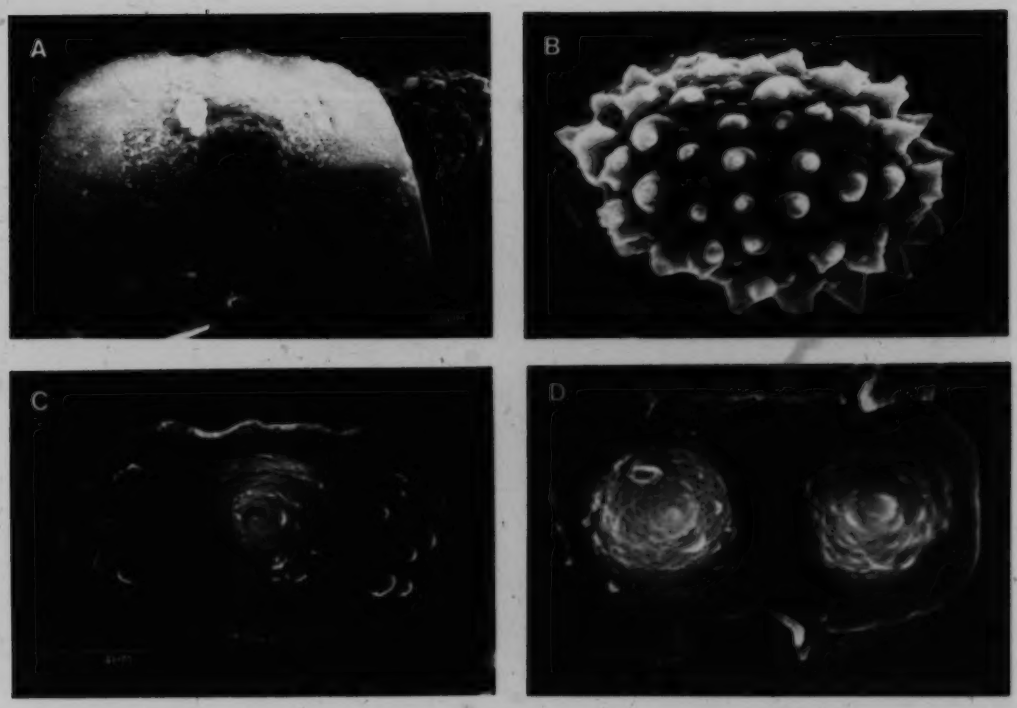


Figure 20 - Sedge phytoliths in SEM. A: Scirpus tuberosus, scutiform phytolith in lower view, showing coarser biosilica tertiary structure around the cavity corresponding to the inside of the protuberance, which indicates that silicification is centripetal. B: Scirpus tuberosus, scutiform phytolith, protuberance unconspicuous, tubercules cochleate covering the upper surface. C: Carex obtusata, scutiform phytolith, protuberance slightly pointed medium, tubercles polarized (generally 6 to 9 in each side). D: Kobresia bellardii, two fused scutiform phytoliths, protuberance large and slightly pointed, many irregular tubercles covering the protuberances.

surface sculpture. From there, silicification continues centripetally; however, they do not form vacuoles, like the grasses (Figure 20A).

A minimum description of sedge t-phytoliths should include the following information:

- Shape of phytolith in upper view: circular, elliptic, square/rectangular, rhomboid. Fused or not.
- Maximum length.
- Maximun width.
- Height.
- Nature of protuberance: unconspicuous, small, medium, large. Pointed or rounded.
- Nature of tubercles: distribution, number, and shape (usually clear only under SEM).

Ground cell c-phytoliths in the Cyperaceae are generally similar to their equivalents in the Poaceae (Figure 18B). They can be usually distinguished by their tabular shape, and commonly spiny sides. Elongated t-phytoliths do not occur in the Cyperaceae, therefore, there is no ambiguity: all elongated phytoliths in the Cyperaceae are c-phytoliths. In other cases, the ground cells themselves are so peculiar that identification is unambiguous (e.g. Figure 18D).

Sometimes stellate mesophyll cells, which are typical of aquatic plants, also produce c-phytoliths (Figure 19B). There are some other phytoliths with restricted taxonomical distribution, such as the hemispherical echinulate or

verrucate bodies formed in transversal walls of epidermal cells of *Scleria* (Figure 18C), which have not yet been properly studied.

The walls of sedge epidermal cells can silicify, totally, or partially (e.g. in sinuosities). In some instances of very restricted taxonomical distribution, very distinct wedge or bridge-shaped portions of the outer wall silicify (see Metcalfe, 1971, for illustrations and distribution).

As I think can be appreciated from this brief overview, the study of sedge phytoliths promises to be at least as fascinating as the grass counterparts.

2.5.4 Other phytoliths

The study of phytoliths in plants other than grasses and sedges is even more undeveloped. However, the works by Cutler (1969), Klein and Geis (1978), Kondo and Peason (1981), Kondo and Sumida (1978), Piperno (1983), Rovner (1971), and Tomlinson (1961, 1969), for example, indicate that a very promising potential also exists in this area.

2.6 Application of phytolith analysis

Phytoliths contain two kinds of encoded information: structural and temporal-spatial. The former is related to an ontogenic-anatomical-ecological reference system, while the latter relates to a space-time context. As seen above, phytolith morphological variables correlate with taxa of the

standard system of biological classification, therefore, also correlating to other ecological and evolutionary redundant information associated with this taxonomy. Furthermore, phytolith morphological variables such as size, or nature of silicification, are directly related to environmental variables. Also, physico-chemical parameters (e.g. stable isotope ratios, and trace element profile), contain direct information about the conditions of phytolith formation, diagenesis, and age. The spatial position of phytoliths in sediments, or soils, encloses information of its own. For example, if phytoliths are found in deep sea samples, or in localized archaeological features, they automatically bear singular connotations. The variation of phytoliths in time, or temporal associations to other fossils, also carry particular information.

The avenues for application of phytolith analysis to decode this multivariable redundant information would then include:

- Provide a robust, conspicuous, and paleontologically durable taxonomic parameter, specially for Monocots.

- Yield data for evolutionary studies of plants and animals, particularly on grasses, sedges, grazers, and omnivores (e.g. hominids).

- Indicate past vegetation (in particular when pollen and other organic remains are not preserved), including graminoid diversity.

- Complement pollen analysis (e.g. by discriminating Poaceae and Cyperaceae further than the family level), and other multivariate paleoecological indicators.

- Aid in paleoenvironmental reconstruction through information related to autoecology, taphonomy, and physico-chemistry (e.g. isotope ratios).

- Trace the evolution, and the ecosystemic proportion of C_3-C_4 photosynthetic pathways.

- Reconstruct diets and paleodiets, through the analysis of feces/coprolites, gut contents, dental tartar, food residues, and teeth abrasion marks.

- Determine diet involvement in pathologies, such as urolithiasis (Bailey, 1981), pneumoconiosis (Holt, 1957), and cancer (Hodson and Parry, 1983; O'Neill *et al.*, 1982; Rose, 1968).

- Unravel archaeological information, for example about domestication of plants and animals, agricultural practice, activities, source of fuel, interpretation of features and storage areas, artifact use, and ceramics.

- Help understanding soil genesis (e.g. grassland versus forest soils), and nature of paleosols.

- Serve as a stratigraphic correlation tool, as do many other microfossils.

- Provide absolute dating by analysis of occluded radiocarbon, or thermoluminescence, when better materials are not available.

- Indicate sediment and soil parent material source.

- Criminal investigations, and forensic applications.

Finally, I hope to have demonstrated that the study of phytoliths deserves more attention than presently devoted, and that its potential is not so remote as usually thought. However, it should not become an isolated field, because the results of phytolith analysis are certainly maximized by integration within a multidisciplinary context of research. I think that the essential areas of phytolith analysis to be developed in the near future, are the deepening of research on phytolith ontogeny, in grasses and other plants, as well as their evolutionary significance. The taphonomy of phytoliths needs immediate investigation, particularly to determine if there are unique problems to interpret paleoenvironments using these microfossils. Parallel to this, the survey of phytolith occurrence and variation in the Plant Kingdom, should be continued and accelerated.

3. Pleisto-Holocene mesoglacial ecology of Beringia: a first contribution from phytolith information

3.1 Introduction

As it is common knowledge, there have been several glacial-interglacial cycles during the geological history of our planet. The last and best known of them started at the end of the Tertiary, and continued throughout the Quaternary. Between the dynamically quasi-stable full glacial and full interglacial modes, there were considerably long transitional periods, spanning approximately the time that the glacial ice-sheets take to form or disintegrate, which I call mesoglacials. These were times of profound and rapid worldwide climatic, physiographic and biotic changes. The mesoglacial that occurred at the Pleisto-Holocene boundary - after the last full-glacial (about 16,000 BP) and the beginning of the present full-interglacial (about 8,000 BP) - was a time of dramatic changes in the Ecosphere: the climatic patterns modified completely, large glaciers and ice-sheets waned, the sea level rose at least 100m inundating vast stretches of coastal areas, qualitative and quantitative floral and faunal changes were very extensive. In addition to these global events, the New World witnessed the colonization by humans, massive extinctions of megafauna, and the biogeographical isolation from the Old World by submergence of the Bering land-bridge.

The Bering paleoisthmus formed several times during the Cenozoic glacials, as a consequence of the lowering of sea level due to water being locked up in continental ice. This communication link between the Palearctic and the Nearctic remained by and large unglaciated, constituting an important biogeographical synapsis. This opportunized a pathway for contingents of fauna and flora. At some point during the last time it formed, roughly between 25,000 and 10,000 BP, it also served for Asiatic humans to cross westward, and start the colonization of the Americas. In reality, when the bridge was in existence, during glacial and part of mesoglacial times, there was a continuous mass of unglaciated circumboreal Holoarctic land from Iberia to the Yukon.

The focal point of this chapter will be the area of this huge biome between the Lena and the Mackenzie basins, which is widely known as Beringia (Hopkins, 1967, 1972, 1979; Hopkins et al., 1982), in particular North American (or eastern) Beringia. This area is of particular relevance when studying the mesoglacial events cited above, and to understand the initial human occupation of the New World, for this was the main ecological filter to folks before reaching the more amenable lands south of the ice-sheets. In this particular, there is an ongoing and heated debate as to when and how the New World was peopled, and Beringia is, obligatorily, at the very center of the problem.

Judging from the published evidence for early humans in America (e.g. Bryan, 1978; Shutler, 1983; West, 1983), and my own experience with most of the relevant sites, at present time there is no clear indication for peopling of South America earlier than 13,000 BP, or for North America (including Beringia) earlier than 16,000 BP. Most of the problems with the evidence claimed to be earlier than this falls into one of the following categories: evolutionary, paleontological, paleoecological, or cultural contradiction; questionable artifacts; stratigraphic problems; taphonomic problems; questionable associations; possible carbon contamination; possible old carbon used for fires; dates on bone apatite; small samples or dates with large errors; and questionable dating techniques. Considering that there is also no firm evidence for the occupation of northeastern arctic Siberia at least before 16,000 BP, and that physical anthropological data indicates relatively small amount of microevolutionary changes since the first Asians entered the New World (e.g. Turner, 1983), it seems more plausible, until clearly refuted, to work with the hypothesis that humans arrived in eastern Beringia not earlier than about 16,000 BP, that is during the beginning of the last mesoglacial. On the basis of physical anthropological evidence, it seems that there were at least two major migratory episodes from Asia: an earlier one, which brought "atypical" Upper Paleolithic traditions, and a later one after about 11,000-10,000 BP, which brought microblade

traditions. The earlier migrations would have originated most of the paleo-indian populations of the Americas, while the other would have originated populations that later developed, or acquired adaptations to exploit the talassocycle (Eskimo and Aleut). Populations of the Pacific Northwest might have resulted from hybridization of those two original groups of migrants. Therefore, for the purposes of this chapter, the working hypothesis will be that humans became part of the eastern Beringian ecosystems during the last mesoglacial.

Along with the arrival of humans, another natural event that is recurrently controversial among Quaternarists was the massive and quite abrupt vanishing of megafauna in the American mesoglacial. Again, Beringia provides a wealth of empirical data to help unravel this paleoecological enigma.

The present generalized physiognomy of the vegetation in the interior of the Beringian area is predominantly: forest in the southern portion (spruce-dominated in Alaska and the Yukon, and larch-dominated in Siberia); and tundra in the northern portion (or higher elevations to the south), with dominance of shrub-birch, sedges, ericads, mosses and lichens. River bars, Holocene terraces, and flood-plains commonly have willow and alder. Higher mountains and the high Arctic have alpine tundras and polar deserts. More continental, dry and well drained areas of Siberia, have a steppe vegetation dominated by a diversity of grasses, sedges, sage, and herbs (Yurtsev, 1982); and well drained

south-facing slopes of the Yukon and Alaska also have a vegetation cover of grasses, sage, and herbs (Young, 1982). It has been suggested that these presently restricted steppes represent relics of the more extensive Pleistocene steppes.

There is a reasonable agreement among the authors that, during interglacial and interstadial times, the vegetation of the area was more or less similar to the present one, or in some instances even more mesic (e.g. during the last interglacial). Concordance also exists that, since the last mesoglacial started, a generalized ecological succession was set in progress, first with an increase in shrub-birch and heaths, then spruce (North America) or larch (Siberia), alder and other taxa widespread in present boreal subarctic/arctic environments. However, there is no general concensus about the nature of the vegetation during the last full glacial and late glacial (beginning of last mesoglacial).

Pollen studies conducted since the fifties indicate that a treeless vegetation, dominated by grass, sedge, sage, and a variety of herbs, was widespread in Beringia during the last glacial (for reviews see papers in Hopkins, 1967, and Hopkins et al., 1982). Other indicators, such as fossil mammals (Sher, 1974; Péwé, 1975; Harington, 1978; Guthrie, 1982; Matthews, 1982), plant macrofossils (Matthews, 1982), and fossil insects (Matthews, 1982), tend to confirm the pollen record. It is in the interpretation of this record to

reconstruct the terrestrial ecosystems, particularly density and productivity of the vegetation, that conflicting hypotheses exist.

Hypothesis 1 - The full-glacial vegetation would have present day analogs, and be preponderantly similar to present depauperate, and highly discontinuous fell-field tundra (Cwynar and Ritchie, 1980; Ritchie and Cwynar, 1982), or something comparable to the vegetation of north Banks Island and north Victoria Island (Ritchie, 1984). This is based principally on the presence of certain arctic-montane herb pollen, and calculated low pollen influx. This kind of vegetation cannot support a rich megafauna, therefore, this hypothesis predicts that the fossil megafauna do not represent a full-glacial biocoenosis, or that the megafauna was very rarefied. Radiocarbon dates indicate that at least bison, horse, mammoth, caribou, musk-oxen, moose, and sheep were part of a full-glacial biocoenosis; however, the possibility of a rarefied megafauna cannot be dismissed with available data. In this hypothesis, the late-glacial dominant vegetation is reconstructed as a slightly more productive herb-willow tundra with sparse dwarf birch, similar to the present vegetation of south Banks Island and south Victoria Island. Also during late-glacial times there would be more extensive lowland wet meadows and willow shrublands. Another prediction from this hypothesis is that there will be a low diversity of grasses, and practically only Poeae will be represented. This can and will be tested

by phytolith analysis further on in this chapter.

Hypothesis 2 - The full-glacial and late-glacial vegetation would have no modern analogs in the arctic or sub-arctic. It would have been a productive and relatively homogeneous grass-sedge-sage steppe (Guthrie, 1968; Matthews, 1976) and, according to Guthrie (1982), possibly even including C_4 grasses.

This "steppe-tundra", "arctic-steppe", or "mammoth steppe" hypothesis predicts a relatively high density of megamammals, which cannot be tested properly at present time (insufficient dates on fossils).

The part of this hypothesis, which proposes the presence of C_4 grasses as a significant component of the "steppe-tundra" (Guthrie, 1982), predicts that mammalian tissues (particularly bison) will have $\delta^{13}C$ reflecting the dietary proportion of those grasses (see Note 4). Bombin and Muehlenbachs (in press) tested this hypothesis by analyzing carbon isotope ratios of mummified tissues from practically all available Beringian samples. These included fossil remains of bison, equids, mammoth, caribou, musk-oxen, moose, wholly rhino, and other undetermined species, found in Alaskan and Siberian permafrost since last century. The results of this research indicate that only C_3 plants were a significant dietary item for the specimens studied. Also, there was no significant isotopic difference between bison and the other megaherbivores, to justify any idea about co-evolution of bison and short-grass C_4 grasses in

Beringia. The presence of C_4 grasses in Beringia can be further tested by phytolith analysis, because the Chloridoideae and Panicoideae produce very diagnostic t-phytoliths (e.g. Figs. 10A, 10C, 13B and 13D).

The homogeneous "steppe-tundra" hypothesis would also predict that phytoliths should be abundant but not very diverse, if there was a marked dominance of certain grasses.

Hypothesis 3 - Glacial and mesoglacial vegetation would have been a mosaic of sub-systems (tundra, steppe, wet meadows, and willow shrubland), different in composition and productivity (overall productivity higher than hypothesis 1), controlled by variation in substrate, topography, and microclimate (Matthews, 1982; Schweger, 1982). More productive steppes and meadows would have been important components of the lowlands. As a whole the vegetation of this extinct biome would have no modern analogs; however, each sub-system could have a present similar counterpart elsewhere (some remaining in the area as relicta). This hypothesis will predict a diverse megafauna, and different fossil records depending on site. If the phytolith record reflects with reasonable fidelity the graminoid component of the vegetation, this record would be also predictably diverse between sites, but relatively homogeneous within sites.

This being a pioneering work in phytolith analysis as a paleoecological tool in Beringia, in addition to testing the hypothesis above, it will also serve as pilot study to

establish the representativeness of fossil phytoliths, and applicability of the method in the area. Detailed studies site by site, and the preparation of an atlas-key for Beringian phytoliths are in progress, and expected to be submitted for publication within a year.

3.2 Material and methods

To serve as the basis for understanding the fossil record, I initiated a reference collection of grass and sedge phytoliths from the Beringian area. The selection of genera and species was guided by Hultén (1968). Specimens were collected in the field and obtained from the following herbaria: Department of Plant Science (University of Alberta), Northern Forest Research Center (Edmonton), Smithsonian Institution (Washington), and Komarov Botanical Institute (Leningrad). So far, I have studied about 150 circumboreal species, covering most of the grasses and important sedges from the Beringian area, and pertinent grasslands in Alberta and the northern High Plains. All have been observed by optical and SEM microscopy.

In 1978, I collected samples from fluvial sediments from the Old Crow Basin, Yukon. Later on, I obtained coprolites and fossil matrix samples from the American Museum of Natural History, Smithsonian Institution, and National Museums of Canada. However, the most pertinent set of samples for this study, was received from Thomas A. Ager (U.S. Geological Service), including core sediment samples

from Harding Lake (Tanana Valley, Alaska), Eightmile Lake (Northern Foothills, Alaska Range), Birch Lake II (Tanana Valley, Alaska), Lake George (Tanana Valley, Alaska), and Zagoskin Lake (St. Michael Island, Norton Sound, Alaska). All the phytolith samples were prepared and analyzed according to the respective methods described in chapter 2, section 2.4.

3.3 Results and Discussion

The fluvial sediment samples from the Old Crow Basin were almost sterile of phytoliths, despite efforts to concentrate biosilica from large samples, and did not produced any results pertinent to the testing of hypotheses concerning the mesoglacial vegetation of Beringia. Samples from similar fluvial sequences in the Yukon, collected by other researchers and submitted to me for analysis, also have proven almost devoided of phytoliths. The absence of other siliceous microfossils, such as diatoms, and the presence of highly corroded sponge spiculae, suggest that phytoliths and other fossils of similar composition have been dissolved during diagenesis. If this is a generalized phenomenon, fluvial sediment samples from Beringia might deserve a secondary priority in future studies. Other fluvial sediments that I have studied (from South America, for example), were exceptionally rich in phytoliths; therefore, this kind of diagenetic impoverishment is not a universal problem in fluvial deposits. All the other samples

(lake sediments, muck, and coprolites) contain excellently preserved phytoliths.

The samples from Harding Lake (Nakao, 1980; Ager, 1983) covered all the pollen zones established by T. Ager, and a summary of their percentage phytolith content is given in Figure 21. The phytolith record can be reasonably discriminated if subdivided by the pollen zones. The diatoms from the same samples are being studied by E. Bombin, and there is also a good agreement with their record. A multivariate analysis of the phytolith, pollen, and diatom records is in preparation.

For the purpose of testing the hypotheses about the nature of the vegetation during the first part of the mesoglacial, the only pertinent data at this point is the record from the herb zone. There is a diverse assemblage of phytoliths in the samples from this zone (70 morphotypes), including different bilobate and trilobate t-phytoliths which correspond to *Glyceria* (Figures 14A and 14C), *Stipa* (Figures 11B and 13A), and perhaps *Danthonia* (Figure 10B), as well as cymbiform t-phytoliths from *Koeleria* (Figures 9C and 15B). All of these genera are not part of the present arctic assemblages. They are represented today in more southerly temperate steppes. This phenomenon of presently temperate biotic elements being present in Beringia during glacial and mesoglacial times, has been already documented by Matthews (1982). No C_4 grass phytoliths were observed. The details of the entire analysis are being prepared for

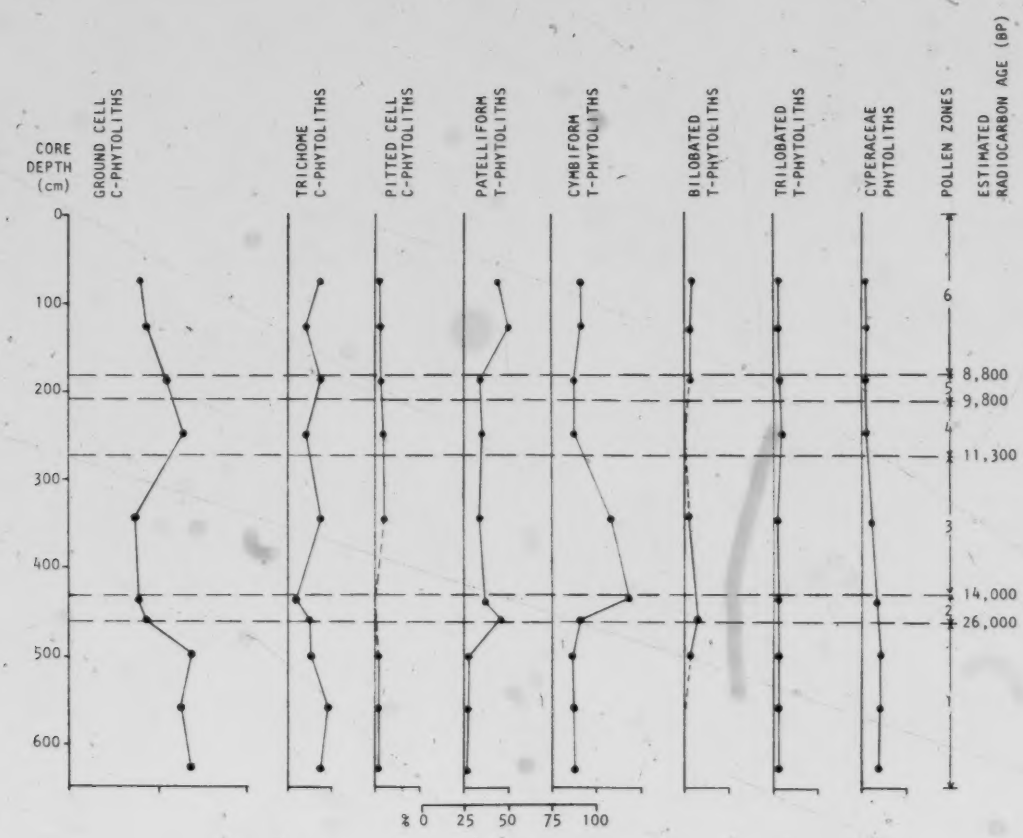


Figure 21 - Summary phytolith diagram from Harding Lake, Tanana Valley, Alaska. Pollen zones: 1, Picea-Ericaceae-Sphagnum; 2, herb; 3, Betula; 4, Populus-Salix; 5, Picea-Betula; 6, Picea-Alnus-Betula.

publication integrated with the diatom (by Elisa Bombin) and pollen (by Thomas A. Ager) records. The basal zone of this lake, separated from the herb zone by an unconformity, corresponds to the last interstadial. An interesting feature of the record in this basal zone, is that despite the very low percentages of grass pollen in some samples, phytoliths are very abundant, indicating the possibility of a biased pollen record in those samples.

The samples from Eightmile Lake (Ager, 1983) also cover all the pollen zones, and a summary of their percentage phytolith content is given in Figure 22. Here, it is equally possible to discriminate relatively well the phytolith distribution from the pollen and diatom zones. The herb zone, of interest for testing the vegetation hypotheses, also contains a diverse assemblage of phytoliths (65 morphotypes), but of different overall composition in comparison with Harding Lake. It also has different bilobate and trilobate t-phytoliths corresponding to *Glyceria*, and *Stipa* (only in the basal sample), and in this case it contains pitted-cell c-phytoliths cf. *Agropyron* (Figures 16C and 16D). No C_4 grass phytoliths were observed. The same as in the case of the previous lake, a detailed paper about Eightmile Lake is in preparation with E. Bombin (diatoms) and T. Ager (pollen).

Only the herb zone samples have been analyzed from Birch Lake II, Lake George (Ager, 1975), and Zagoskin Lake (Ager, 1983). All of the samples contain diverse assemblages

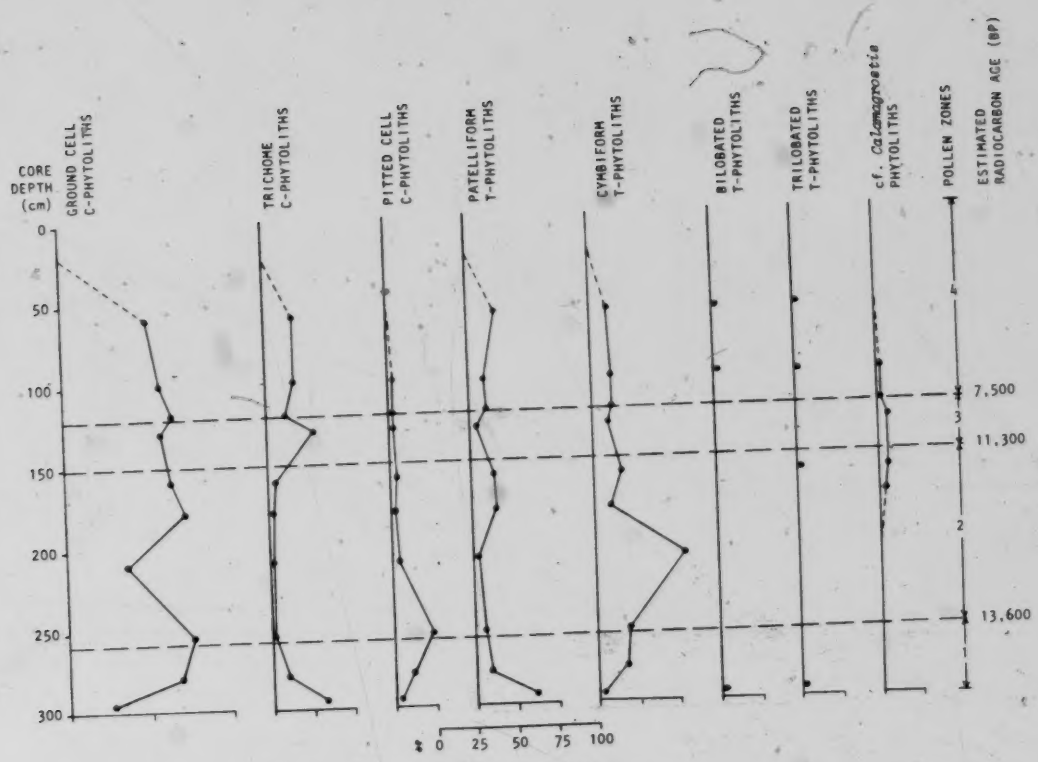


Figure 22 - Summary phytolith diagram from Eightmile Lake, Northern Foothills, Alaska Range. Pollen zones: 1, herb; 2, Betula; 3, Populus-Salix; 4, Picea-Alnus-Betula.

of phytoliths, within and between samples (about 200 morphotypes have been identified so far from the herb zone of Alaskan lakes). All of them contain different bilobate and trilobate t-phytoliths (cf. Meliceae, Stipeae, Danthoniae, and Triticeae). None of the samples have phytoliths indicative of C_4 grasses. The herb zone of all the lakes studied present a variable degree of redundancy with soil reference samples from the Albertan Peace River steppes (Moss, 1952), but this has to be further investigated.

Among the coprolite samples already analyzed, only one is pertinent to the testing of Beringian glacial vegetation hypotheses. It is a ground squirrel coprolite from the Fairbanks area (AMNH Frick Col. A81-2026A), which has a radiocarbon date of 18,230 ± 410 (QC-668). It contains a variety of phytoliths from at least ten species of grasses, two species of sedges, and *Equisetum*. However, the most interesting feature of its assemblage is the very high percentage of *Agropyron* "crown cell" c-phytoliths (90%), and the presence of trilobate t-phytoliths cf. *Stipa*. Husks of Triticeae contain almost exclusively "crown cell" t-phytoliths; therefore the coprolite indicates a diet rich in seeds of *Agropyron*, and probably represents a late summer or fall meal.

These preliminary results of the herb zone phytolith assemblages are, as a whole, incompatible with hypothesis 1. The sole diversity of phytoliths is robust enough to reject

this hypothesis, because there is no present wet meadow, fell-field or herb tundra analog redundant with this information. Furthermore, the presence of *Agropyron*, *Stipa*, *Danthonia*, and *Koeleria*, in addition to Meliceae, Aveneae, and Poeae, cannot be reconciled with the reconstructions proposed in hypothesis 1.

With respect to hypothesis 2, although the possible taphonomic problems with phytoliths are unknown at present, as it stands, the phytolith record speaks against a homogeneous steppe throughout Beringia, and reinforces the carbon isotope indication that C_4 grasses were not present in glacial or mesoglacial Beringia.

The predictions of hypothesis 3, are more in accordance with the phytolith record; however, the within habitat diversity of grasses reconstructed from phytoliths, suggest a more varied assemblage than that predicted by hypothesis 3. Therefore, a modified hypothesis 3, including diversity within habitat, is the best approximation to accomodate the phytolith record, and perhaps all the fossil data. Again, caution in necessary in the interpretation of this record, until more is known about the taphonomy of phytoliths.

The complete data from lake stratigraphic cores, which is still being interpreted, suggests preliminarily that even after the onset of the Birch Zone, throughout the Poplar-Willow Zone, changing but diverse and abundant assemblages of grasses continue to be widespread in Beringia. Therefore, the explanation of other

paleoecological events such as the extinction of mesoglacial megafauna in Beringia ask for multivariate models (Note 5). Coincidental or not, it is interesting to note that the end of the Paleoarctic Tradition (Jennings, 1978) occurs more or less synchonously with the decrease in grass phytoliths from the samples, at the end of the mesoglacial.

3.4 Conclusions

The results from this initial study of fossil phytoliths from Beringia indicate that they hold more than just potential, to help reconstructing past ecological events of that important paleobiogeographic region. The following are the conclusions of this preliminary work:

a) Quaternary fossil phytoliths are abundant and widespread in non-fluvial deposits of Beringia; where they provide important and unique paleoecological information.

b) The phytolith record from Herb Zone samples, and contemporaneous coprolites, can be used to test conflicting hypotheses about the nature of the glacial and late glacial vegetation. Although more needs to be investigated about phytolith taphonomy, at this point the results indicate that the physiognomy of the plant cover at that time is better described as a vegetation mosaic, where steppes were an important component. Moreover, if the phytolith record indeed reflects accurately the graminoid component of the vegetation, the steppes would have probably displayed within and between habitat diversity, constituting a biome without

present analogs.

c) Phytolith data confirm the carbon stable isotope indication that C_4 plants (which have diagnostic phytoliths) were not a feature of the herb zone steppes.

d) It appears that different grass-rich habitats continued to be available after the herb zone time, throughout the mesoglacial. This could have important paleobiological and cultural implications.

e) The stratigraphic variation of fossil phytoliths is correlated with other traditional indicators, such as pollen and diatoms.

NOTE 1: Thoughts on information evolutionary theory and related topics

Prolegomena

Evolutionary theory and approaches have not been at peace since that July 1, 1858, when the papers of Darwin and Wallace were read at the Linnean Society. Although they had different approaches, Wallace putting emphasis on variation and Darwin on natural selection, the latter polarized work to come (even by Wallace later on). Natural selection became the pivot of much controversy for almost a hundred years, until the "modern synthesis" was produced by Darwin's defenders. This "synthesis" was so full of data from different fields, mathematical formalisms, and supported by so many eminent scholars from important centers, that it was able to overwhelm most biologists, or at least make them not willing to risk their careers by contradicting the Establishment. So, for decades most biologists were educated (brain-washed?) under a strict Darwinian framework. Everything was explained away mainly by adaptation through natural selection. The core of the theory was so simple and easy to identify with that it became rapidly popularized. Even non-biologists, such as social anthropologists and political scientists, borrowed Darwinian ideas to "explain" their problems. And this came at no better historical time than the post-Victorian industrial world.

The atmosphere of dissent of the 1960's and 70's spreaded also to Biology, and some prominent scholars started to point out the serious problems of Darwinism. The presumably gradual pace of evolution, already criticized by D'Arcy W. Thompson earlier in the century, came under attack with renewed impetus in face of the fossil record; and to some, genetic drift was elevated from exception to rule (reviews in Vrba, 1980; Stanley, 1981). Natural selection was seriously questioned (reviews in Grassé, 1977; Rifkin, 1984). Epigeneticists claimed their place (Løvtrup, 1981). And even a new wave of creationists joined the bandwagon and helped attacking Darwinism.

So, in the 80's, evolutionary ideas are again in turmoil, but a unifying theory of evolution is still lacking. What follows is an embryo of a candidate to such status. The key to unification is believed to be in the realm of information theory, therefore, new and reinterpreted old ideas are presented here within a glossary-like informatic approach. These ideas cover important topics to Anthropology, such as mind, culture, and human evolution, as well as to Ecology, such as niche. Other branching concepts are given to show the unifying power of the information approach, and indicate areas of potential theory expansion. Certainly information theory, game theory, cybernetics, and topology can contribute in the future to elaborate more formal mathematical versions of aspects of the evolutionary theory. Admitedly, to be easily

comprehended, the substance of this note would have to be greatly expanded (a project for future work). However, within the concisely programmed scope of the thesis, only the bare essentials and some ramifications are presented in this sketch. The areas of interest for the other chapters will become better explored, though, as the reader progresses along.

When Darwin first presented his ideas on evolution at the Linnean Society, he wrote: "This sketch is *most* imperfect; but in so short a space I cannot make it better. Your imagination must fill up very wide blanks." Conversely, it is hoped that this sketch, even *most* imperfect, will fill up very wide blanks in your imagination.

Corpus

Our **Universe** is ultimately monistic, because it is composed of transmutable states: space, time, matter, energy, and information (and their symmetric counterparts). None of these five "first principles" is homogeneously distributed. In contrast with a nebula, for example, life forms contain concentrated information, matter, and energy, operating on small space and time reference systems.

Information is any property of space, time, matter, energy, and of itself, capable of being transmitted, received, and stored. Information emanates from states and from relationships. Anything in the Universe can be represented by its information (*Informare* = to give form

to). All we know about the Universe comes through its information. What differentiates information are the different probabilities within a context.

Information **epigenesis** is the generation of information from information. For example, there is not enough information in the DNA of our zygotes to give all the instructions to build even the brain, let alone the whole adult body; most of the information is epigenetic, and only the initial program of the hierarchy (DNA) is necessary to have the process started on the complex organization pathway towards the complete organism (**ontogenesis**), the rest is produced along the way from each precedent state. Epigenesis involves synformation, selformation, and syllogiformation.

Synformation is the transformation of information by information. A change of animal coloration as a response to environmental stimuli is an example of synformation.

Selformation is the self-organization of information (e.g. in our mind).

Syllogiformation is a combination of probabilistic information minus the redundancy in common (e.g. if A>B, and C>A, then C>>B, where A is redundant). The resultant information is also probabilistic.

Probability is a relative expression of the information about existence versus non-existence (*yes/yes+no*) or vice versa. It provides information about what is between *yes* (prob.=100%) and *no* (prob.=0). Probability depends on randomness. Proportion between probabilities is also

probability.

Transition probability is the probability of one state following another in a chain of states (e.g. ontogenetic chains). The transition probabilities of a system depend on the transition probability of its components. Transition probabilities can be controlled by feedback from other states of the epigenetic chains (e.g. hormones and enzymes in ontogenesis).

Rate of transition is the amount of epigenetic transition during a given time. It is equal to the relation between the probability of a state to stay the same and the probability that it will change during a given time. The rate of transition can be controlled by feedback from states of the epigenetic chains, acting on transitional loops to stay the same.

Information can be measured by relating to a reference system, usually a logarithm base. The logarithm of the inverse of probability is a measure of information (**instantaneous information**). The **macarthur** (Van Valen, 1973) is an example of instantaneous information.

The logarithm of the inverse of transition probability is a measure of **transition information.**

In a system of *i* components, the **average information** ("H", "entropy", "amount of uncertainty") in information units/component is represented by:

$$\sum_i \text{Probability}_i \times \text{Information}_i$$

where Information_i = -logarithm of Probability_i.

Average information is a function of randomness, independence, and number of components. The maximum average information of a system occurs when all the components are independent and equiprobable. Average information has been used to represent ecological diversity.

Explanation is the justification for the average and actual information of components of a system. **Theory** is generalized explanation.

Error occurs when information does not fall within its probability, that is when non-probability occurs.

Distortion is an intrinsic change of transmitted information.

Noise is an extrinsic change (perturbation) of information being transmitted.

Interference is an extrinsic addition or subtraction of similar information to a message being transmitted.

Distortion, noise, and interference cause errors in transmission of information.

Stochastic processes are those in which the sequence of states depends on probabilities. A stochastic process is **ergodic** if the transition probabilities from one state to the next are constant (e.g. Markov chains); otherwise they are **non-ergodic**. For example, **ontogeny** is the stochastic sequence of non-ergodic epigenetic chains to form organisms, from the parental replicated nucleic acids to the mature individuals.

More precisely then, Earth **life** is a state of matter-energy and information, within a space-time framework, where proteins are formed usually under the control of a nucleic acid blueprint (prions seem to be an exception) in an aqueous medium. This is a necessary and sufficient definition of life, because all the other components of living things are an epigenetic corollary of the proteic set and organization.

Life is also heterogeneously distributed in space and time, in quanta called **organisms.** Each organism is the product of a unique interaction between its genetic blueprint information (**genotype**) and all the other information received or generated by the organism during epigenesis. Organisms are ephemeral, but their genotypes or part of them can usually be duplicated and transmitted to their descendants. However, during this process the original genetic information is distorted to a variable degree (e.g. by mutation, contamination, deneutralization, or recombination of genes), or combined with other information (sexual reproduction). Information is further modified from the original by transmission noise, when the nucleic acid code of the copies is being translated into proteins (e.g. by environmental influence), so the completed progeny (**phenotypes**) is not identical to their parents, because it incorporates errors from genetic distortion and environmental noise/interference. Actually the phenotype can change its own information independently of the genotype by

interaction with the environment and, although these changes are not (?) transmitted genetically, this can prevent the transmission of otherwise viable genetic distortion. Each organism is a mosaic of such changes in different **evolutionary units** (e.g. macromolecules, structures, organs), and at different times. With the passage of time, in successive generations, the original genetic information of time zero is further and further distorted, and this explains the variety of life forms. If genetic information were never distorted there would have been no evolution, and there would be only exact copies of the first formed organisms on Earth.

The origin of multicellular organisms, for example, could have occurred if a genetic error made a cell reproduce into two different kinds of cells, which were viable only by sticking together. If successful, they will reproduce the same error again and again, making it systematic. At this point it is no longer an error because it has a definite probability of occurrence. If this process keeps reoccurring, and other successful "wrong" cells are generated, together with channels of communication among them, it will result in multicellular organisms with different kinds of cells, which only can live by sticking together, integrated by closed circuit transmission of information.

Informon is an information set (package), represented by **symbols** (operational units of information), which allows

to operate with information in a very economical way. Letters and words are examples of informons. Imagine how much information is synthesized in words like universe, life, culture, and love. Musical and mathematical symbols are other examples of informons. Combinations of informons do not simply add their information, they epigenerates more information sometimes with unexpected and powerful content (**synergy**). Poems and symphonies illustrate this well. Informons have real existence in the realm of information. Therefore, the notion of abstract ("removed from concrete reality") is wrong, because "abstract" information is as real as space, time or matter-energy.

System is a set of components that epigenerates idiosyncratic information. **Components** are any discrete entities such as informons, states, events, and relationships.

Black-box is a system about which it is not known how its epigenetic information was, is, or will be generated.

System **efficiency** is the ratio between the rates of output to input information.

Language is an operational system of information coded into informons, which are generally arranged or arrangeable unidimensionally.

Redundancy is the presence of equivalent information in components of a system. Is is measured by the proportion of information necessary to attain maximum information, i.e. Inform. max - Inform./Inform. max (Young, 1971). Redundancy

between sets of related information is evaluated by correlation coefficients.

The information **capacity** of a component or class of components y is given by:

$$\text{Reference constant} + \text{Dimensional or Frequency constant} \times \text{Information}_y$$

where Information_y = -logarithm of $1/y$.

Einstein's energy-mass relation, Boltzmann's entropy in statistical mechanics, Huxley's allometric relation, or the species-area relation are but some of the equations that can be transformed and represent information capacity. The last two examples are of fundamental interest to evolution. This transdisciplinary unification is what makes working with information transformations extremely powerful in understanding the Universe holistically. Perhaps the solution to finally producing a unified theory of fields resides in using information transformations and concepts; after all the geometry of curved space-time is in the realm of information. Furthermore, space, time, matter, energy, and information have information constantly emerging from them, which our thinking system is capable of manipulating, hence the unity of the mind with the universe. This unity has been one of the most persistent philosophical problems, and many thinkers have tried to tackle it unsuccessfully from Antiquity to the 80's (e.g. Bateson, 1980), because they failed to see clearly that information provides the real "missing link."

Mind is, then, the thinking system of the human brain. It is an information receiving, storage, processing, and transmitting system. **Thinking** is the dynamic arrangement of information in the mind (or equivalent). Information organizes in the mind to the point of perceiving and understanding itself. Most thinking is done by unidimensionally arranged information (language). However, the mind is capable of transforming unidimensional into multidimensional information, and vice versa.

The first step in thinking is the accumulation of information (**memory**), a process that continues throughout the life of humans. In this process, information is made more or less rapidly available by degree of redundancy. An important part of this process is the formation of cultural algorithms (**enculturation**), which is characterized by continuous reinforcement through redundancy, directly from humans with already redundant cultural algorithms, or indirectly from their archives (external memory).

Algorithms are characterized by rigidity and tendency to repel competing algorithms. Therefore, after a cultural algorithm has been loaded and sculptured in the mind by enormous redundancy, it will tend to repel other algorithms non-redundant with it.

After there is a certain amount of information load, three kinds of thinking become established at the conscious level: algorithmic, non-successional epigenetic, and successional epigenetic.

Algorithmic thinking works by comparing information to an algorithm (e.g. cultural algorithm) in search for redundancy. Most behavior is produced by this type of thinking. It expedites a behavioral reaction but, if the algorithm is not appropriate for the situation, error is certain.

Non-successional epigenetic thinking emerges from spontaneous selformation, synformation, or syllogiformation.

Successional epigenetic thinking starts by syllogiforming a **hypothesis**, from information already in memory or gathered through observation (with or without an auxiliary technique). From the hypothesis a **prediction** is selformed and evaluated by selformed **tests**. The results of the evaluation (+ or -) will synform the hypothesis, and the successional thinking cycle can restart again. The epigenesis of hypotheses by syllogiformation is called **induction**, and the epigenesis of predictions by selformation is called **deduction**. The so called **scientific method** of thinking is an example of this. It is more acceptable in conventional scientific research because of its low error, although it could be sometimes a very slow process. If a hypothesis is proposed by selformation, it usually needs to be syllogiformed *a posteriori* to be accepted in Science. The same is true when a prediction is selformed without a previously syllogiformed hypothesis. Hypotheses are probabilistic statements that epigenerate probabilistic predictions. **Tautology** occurs when the prediction

information is totally redundant with the hypothesis information. If a prediction is made into its hypothesis a tautology will exist.

Other basic mechanisms of the mind are the capability of blocking information from consciousness and erasing information.

If **culture** is the mind's set of information algorithms used to interact with the Universe, a cultural tradition is the presence in space-time of a set of minds with redundant culture. Culture serves as a meta-systemic codex for the individual, including a "world view" and a repertoire of norms for acting. Mathematical rules, algorithms, deterministic and stochastic laws, law-like and empirical generalizations, logico-philosophical laws, cosmologies and cultural laws (myths, taboos, and beliefs, including religion), all contribute to form culture, and vice versa. Or, in a more general context, so do Science, Art, and Philosophy. **Science** being the formal symbolic arrangement of information intended to represent the states and relationships of the Universe(s). **Art** (not craft) being formal symbolic arrangement of information intended to generate emotions, which are also a particular class of information intuitively known by all of us. In a more formal sense, **emotions** (or feelings) are perceived information about the upsetting of homeostatically controlled states of the mind, **Philosophy** being the formal thinking about thinking and ultimate truths. Art, Science and Philosophy

are all related by thinking.

The evolution of the mind's capacity of storing and manipulating information is dependent on the evolution of the brain, which is the substrate system of the mind. However, the mind cannot be completely understood by solely studying the anatomo-physiology of the brain, because once the mind is epigenerated it epigenerates the capacity to epigenerate information on its own. The study of the evolution of the brain serves to elucidate the kind of platform of organization necessary to epigenerate the mind and its means of communication.

The evolution of the mind is characterized by its tendency to independization from the rest of the information universe with increasing information loading, which is actually a property of any complexifying information system.

The evolution of the mind brought about the problem of correcting the resonance of redundancy. In large extent culture is the reference algorithm to correct selformed resonant redundancy. The uncorrected resonance can lead to **paranoia**. Selformed information itself also has to be corrected homeostatically, or else the mind will be overloaded with selformed information, which takes over supremacy of thinking (**schizophrenia**). Partial uncorrected resonant redundancy produces **neurosis**. Saturation of the correction mechanisms results in **stress**.

Another property of the mind is the selformation of informons. **Taxonomy** is the establishment through

successional thinking of sets of informons defined by their redundancy, and separated from each other by their non-redundancy. Taxonomic informons can usually be clustered hierarchically into informons of higher order, until there is only one informon of the highest order. The Linnean classification is an example of such taxonomy. Taxonomies synthesize information by condensing redundancy. Taxonomies tend to become algorithmic and be incorporated into culture, which rigidizes and makes them repellent of competing taxonomies.

The smaller taxonomic units group individuals with information content closer to each other than to any similarly considered unit. Therefore, the amount of redundancy considered will determine the size of taxonomic sets. **Splitting** taxonomies result from considering little redundancy, while **lumping** taxonomies result from extending the redundancy considered to form the taxonomic informons.

The living are heterogeneously distributed in the Ecosphere, in addition to each individual being different from the other because of genetic and ontogenetic errors. However, the existence of individuals with redundant information makes their taxonomy possible. In the Linnean taxonomy, **species** is an informon clustering individuals with very redundant and, if sexually reproducible, compatible (co-transmissible) information. Therefore, their niches (see definition below) are very redundant. Species are defined in relation to a present space-time reference system.

Paleospecies are similar informons defined in relation to past space-time reference systems, **Technospecies** are those informons grouping organisms created through biotechnology. Species, paleospecies, and technospecies exist as information constructs.

If it is possible to define a species it means that a certain information plan for living was successfully coupled with environmental information.

The size of a species population is an indication of its success at the reference time. The length of the trajectory of population size in time is an indication of the ecological and evolutionary success of a living plan.

In general, the closer the genetic information content of individuals the higher the probability that they will relate by reproduction. Therefore, the lower one puts the individuals in the Linnean taxonomy the closer, in time, they could be related by reproduction. However, this is not always necessarily the case, because of the different frequencies in errors from genotype to genotype. The trajectory of taxonomic units in time (**macroevolution**) is represented by **phylogenies**. Supraspecific taxonomic units contain information about **platforms of organization**, which are the evolutionary steps of organismic complexification.

Ecosystem is a functional unit of interrelated biotic and abiotic information within a certain space-time reference. Ecosystem **succession** is the epigenetic chain of information states of the ecosystem components in

space-time. Succession epigenesis can be culturally channeled by technological use of fire.

Niche of an organism is the set of information about its components. If the variation of information of each component is plotted on a different dimension of coordinates, the niche will be represented by a characteristic multidimensional hyperspace-time. In non-humans, it includes three subsets (subniches): the **somatoniche** (corporeal), the **ethoniche** (behavioral), and the **econiche** (environmental). When the evolution of the brain reaches the human platform of organization and epigenerates the mind, a fourth subniche, representing the mind's information set, constitutes the **mentalniche**, which assumes a prominent role in controlling the other subniches.

The mind is the redundant element that characterizes humans. In nature, only minds can sustain an algorithm so complex as culture. Thus, culture can be used as the redundant element to characterize the presence of mind. Cultural redundancy can be employed to produce taxonomies of mentalniches. "Western civilization" is an example of such taxa.

The niche (N) is contained within the boundaries of a larger hyperspace-time containing all the information variables of our Universe (U). U minus N is the niche complement (NC), therefore, N + NC = U.

Each organism has a unique niche, the minimum difference being on a spacial or temporal variable.

The somatoniche transmits information to the environment and receives information from it (actions and reactions) through the ethoniche. The environmental information related to the somatoniche and ethoniche is the econiche.

The econiche plus the niche complement (only the portion spacially and temporally close to the econiche being significant) is the **environment** (it includes other organisms).

The genotype transmits information to form components of the epigenetic chains that lead to the phenotype. Once the chain is in progress, its components also transmit information, some of it is received back by the genotype or components of the chain in the form of feedback, i.e. regulating further information from them, and some is used to epigenerate other components. The total set of this information is included in the somatoniche. There is noise, distortion, and interference during these transmissions, from the environment and from the somatoniche being created, resulting in errors each time a somatoniche is reproduced. This, plus genetic errors, are the major source of variation in living organisms.

Similar somatoniches can be associated to different ethoniches and econiches, and vice versa. The reciprocal transmissions through the ethoniche are governed by autonomous and conscious comands. They vary from simple physico-chemical reflexes to complex actions and reactions

controlled by the mind. They become increasingly complex with complexification of the nervous system.

Somatoniches can transmit information capable of doing approximately the same as themselves (**asexual reproduction**), or co-transmit information with other compatible somatoniches to produce information capable of doing the same (**sexual reproduction**). The latter process tends to correct genetic errors by redundancy in common. However, this tends to allow accumulation of masked errors that can eventually be transmitted to phenotypes by homozygotic genotypes. Therefore, sexual reproduction increased the possibilities of evolutionary changes by storing masked errors.

The ethoniche is responsible for establishing channels among redundant organisms (species) to promote deme bonding. The ethoniche has a certain inertia to change because to a large extent it is formed by learning from ethoniches formed in a past reference system. Therefore, even if there is a somatoniche change compatible with an ethoniche change in part of a deme, the ethoniche could remain more or less unchanged for a certain time. This could help the maintenance of genetic variation.

Competition is information interference. Therefore, niche differences minimize interference. Internalization of econiche (e.g. by a digestive system and accessories) also minimizes econiche interference.

Organisms live under stochastic conditions, which their existence in part creates, therefore they have a finite **probability of extinction.** An organism will be alive (non-extinct) as long as it maintains a certain proportion of *Yes* to *No* components within the epigenetic chains of its niche. Its probability of extinction at a certain time will be *No/Yes* to the power of *Yes* at that time. In a multicellular organism, for example, there will be a higher rate of *yes* than *no* cells in the juvenile stages, and the probability of extinction of all cells will be *rate of no/rate of yes* to the power of the *number of yes* cells at that time. When the *rate of no* cells is equal or larger than the *rate of yes* cells, the probability of extinction is 1, and the organism is bound to die soon unless the rates change. Each evolutionary unit has also a different probability of extinction.

In an epigenetic chain, the transition from one state to the next (generation of information), for example multiplication of cells, occurs when the transition probability to stay the same is less than 1 (information > 0).

The transition probabilities from one state to the next in the somatoniche change with time (i.e. are non-ergodic). The transition probabilities at the beginning and the end of ontogenic epigenetic chains will tend to 1. The terminating loop (transition probability = 1) is in every case at the extinction state (death). Predation and other similarly

catastrophic events change instantaneously the transition probability of extinction to 1.

Differentiation of cells makes the transition probabilities to stay the same tend to 1. That is, there is almost no information of what to do next, so the cell tends to stay about the same until the transition probability to a terminating loop on extinction approaches 1. The inability of reproducing cells to complete differentiation redundant to adjacent cells within a multicellular organism can result in **neoplasm.** If the neoplasm contains cells capable of producing significant distortion, noise, or interference on internal information it is malignant (**cancer**). **Degeneration** is an increase of the rate of transition to a terminating loop.

A multicellular organism is mature when a certain threshold number of cells have a transition probability to stay the same tending to 1 (i.e. are differentiated). When the organism matures the transition probability of the niche to stay the same also tends to 1. An analogy to this can be drawn for ecosystems.

Transition probabilities can change by genetic errors or errors during epigenesis. **Paedomorphosis** is an example of the former, where the change of transition probabilities, at the epigenetic chains of ontogenesis, produces retention of ancestral juvenile characters in the mature descendants.

Niche efficiency is the efficiency of coupling among the subniches. It depends on the quality and number of

channels per output among the subniches. Niche efficiency is an important factor in controlling the probability of extinction of organisms. Errors of coupling can be minimized by redundancy of channels, but this reduces efficiency.

Not all the possible niche channels are generally in operation at any one time. Also, the somatoniche usually has information not coupled or not efficiently coupled to the ethoniche and econiche (**exaptation**). Changing the niche channels towards increasing efficiency with or without genetic change is **adaptation**.

The boundaries of the subniches vary with space and time, and are elastic. However, their changing configurations change the probability of extinction of the organism. The niche configurations depend on the transition probabilities of its epigenetic chains, and amount of distortion, noise, and interference (extrinsic and intrinsic).

Organisms with efficient niches have lower probability of individual extinction. If they can also transmit viable genetic ~~information~~ without much error, these kinds of organisms will probably last longer in time and/or become common for a certain time.

Disease is a state with niche configurations of lower efficiency than the lower limit of an ideal (healthy) standard. Conversely, **health** is a state with niche configurations of equal or higher efficiency than the lower limit of an ideal standard. There is a minimum threshold for

niche efficiency, below which the probability of extinction increases catastrophically and death (organism extinction) occurs very fast.

Niche **homeostasis** is the attempt to maintain quasi-stable niche configurations through feedback processes.

Change of gene proportions in a deme is not necessarily evolutionary. Only when change in the proportion of genes is not self-reversible, that is when alleles become extinct, it is evolutionary.

The larger the deme the larger the probability of self-reversibility of gene proprtional changes by correction through redundancy. Migration also can cause reversibility of proportional gene changes.

The smaller the deme the higher the probability that an error in genetic information will become redundant through inbreeding, and also that a proportional gene change will not be self-reversible (**genetic drift**). Therefore, any process that reduces the deme size (e.g. catastrophic quasi-extinction, dispersal, dietary supply shortage, environmental bottle-necks, barriers, environmental zonation), marginalizes position on deme, or polarizes sub-demes, will favor genetic information creation or extinction, and vice versa.

Change in proportions of genes in a population is not a good measure of creation or extinction of genetic-epigenetic information through space-time (i.e. of evolution). First,

because proportions of components of the same system have redundancy among themselves (redundant denominator). Second, because it is the genetic-epigenetic information that evolves and not the populations (space-time samples). Third, because gene proportions are not a good measure of epigenesis. Instead, the presence or absence of genes and gene combinations is a direct indicator of evolutionary change. This is not possible to determine in fossils, but the presence or absence of epigenerated information is an approximation.

Sexually reproduced organisms are constantly evolving because the progeny is always different from the parents. However, genetic change seems intermittent in time because there are phases of slow change ("**stasis**") and rapid change.

Slow ("**gradual**") changes in genetic information are not conspicuous in evolution because they are corrected in part by redundancy (there is time for correction of small errors), or because they are suddenly overriden by rapid change. Therefore, the evolutionary record will show overwhelmingly rapid change ("**punctual**").

In reality, if genetic changes are quantic, evolution cannot be gradual by definition. A series of small changes can be mistaken for gradual change, but they are always discrete (punctual).

Evolutionary **trends** are gradients of evolutionary units in space-time. They are seen *a posteriori*, because they are historical pathways in space-time. Trends are the outcome of

stochastic epigenetic chains: after a change occurs the next change has a definite probability of being superimposed on the first one, and so on, forming a gradient. Trends could arise from some genes being more unstable than others. Once changes (e.g. mutations) start in one kind of gene(s) they can continue to be unstable for certain time originating different populations, which are "variations upon a theme". Once a trend is started it tends to be perpetuated until extinction curtails it.

If a trend occurs by changes in transition probabilities at the same point of ontogenic chains, it could give the impression of being gradual in time, even if the transition probabilities change punctually, because if they are plotted against time, any point will fall on the same line (even if there are no intermediate values).

From the set of all possible niches, there is a finite number of niches that can exist for each space-time reference. The probability of niche existence is a function of the probability of the organismic information matrix, and the environmental information matrix. Therefore, an "empty niche" can exist only as a pure informational construct, and not as a representation of naturally patterned information, because if organisms are unique, and niches are information about them, organisms have to exist in order to have a niche. Environmental and organismic information matrices vary stochastically with space and time, therefore the probability of niche existence also varies stochastically

with space and time.

The higher the redundancy between niches the closer their probability of extinction. Therefore, highly redundant niches will have approximately constant rates of extinction (**Red Queen Law** of Van Valen, 1973). Non-redundant niches will have different rates of extinction. The result of random origination of niches combined with constant extinction of redundant niches, and differential extinction of non-redundant niches, is stochastic selection of a different set of organisms for each space-time reference.

Change in genetic information can, directly or indirectly, induce two kinds of changes in epigenesis, namely in the values of transition probabilities, or the number of transitions in epigenetic chains. In the former case, the change in values of transition probabilities causes a **topological transformation** of the somatoniche. On the other hand, the change in number of transitions (and states), either along the chain or by branching (e.g. increase in "germinal centers"), causes a **topological jump** of somatoniche. Combinations of the two are also possible.

In both cases the capacity of information changes: topological transformations alter the dimensional/frequency constant, while topological jumps alter the reference constant. For example, the evolution of the brain from fish to mammal, involved principally topological jumps, whereas the brain evolution in hominids involved mainly topological transformations. D'Arcy Thompson's deformation of

coordinates (Thompson, 1942) also falls within the category of topological transformations, although they are only bi-dimensional representations of morphological components of the somatoniche. Even small amount of genetic change can produce large epigenetic effects through these mechanisms (e.g chimp vis-à-vis humans). This can also be a problem with the use of molecular clocks.

Maturation time depends on the rates of transition during ontogenesis. Organisms can be ranked on a spectrum by rates of transition from "**r-strategists**" (high) to "**K-strategists**" (low). This spectrum is very redundant with other spectra constructed using life histories, and environmental predictability.

The non-transmission of information by reproduction causes extinction of information contained in the non-replicating individual, and this is also responsible for the nature of change through time.

The Darwinian concept of natural selection is essentially fatalistic. It assumes that there are external forces coming from Nature to select the best fit organisms. As a hypothesis to explain evolution it only produces tautological predictions. Epistemologically it has the same value as the idea of phlogiston (it is on fire because it has fire = it is selected because it has selection). In reality, the same as something is on fire due to the properties of its components, the organisms are selected by their own properties during the stochastic process of

living. The environment does not force the organisms to change. The econiche is part of the information of the living organism, without it the organism does not live. If the organisms change genetic-epigenetic information, there is a new probability of extinction associated to the changed organisms, which is dependent on niche efficiency and random chance but, fit or not, all the organisms will go extinct.

"Selective pressures" do not exist, they are, rather, selective probabilities, which are a function of the environment as well as the organism. The environment is not pressing against or for variation, it is just containing variation within certain limits (which in most cases are quite elastic). As a very rough comparison, the environment determines the course and outcome of evolution similarly as a chessboard determines the course and outcome of a chess game.

Coevolution is also a stochastic process, in some cases equivalent to the formation of game coalitions (e.g. symbiosis).

In summary, biological evolution is a stochastic process involving random changes in niche, which results in viable creation and extinction of genetic-epigenetic information through space and time. The genetic information creation can occur by new genes or by new order of genes. The epigenetic information creation occurs by alteration of ontogenetic chains, either changing transition probabilities, and causing a topological transformation of

the niche, or by change in the number of transitions, and causing a topological jump of niche. The rate of transition is controlled by transition probabilities, therefore, a change in rate of transition also causes a topological transformation.

Any niche change alters the probability of its extinction. The random creation of niches with different extinction probabilities through space-time will intrinsically produce heterogeneity. At any one time the Ecosphere will contain log-normally selected sets of organisms with higher redundancy within than between sets. Therefore, selection is not a cause of evolution but an effect of it.

As a general example of application of this theory, it is possible to interpret the main events in human evolution through the following steps (a, b, c, and d in Africa):

a) Around 5 to 4 million years ago topological jumps in the brain area combined with topological transformations of the motor structures of Mio-Pliocene ancestors, produced a larger and more complex brain platform of organization, as well as a fully bipedal platform of organization. Each of these changes included a syndrome of epigenerated anatomical changes. This was the evolution towards the gracile autralopith grade. Another group of related Mio-Pliocene ancestors had topological transformations towards the pongid grades.

It is licit to speculate that the Mio-Pliocene ancestors in common to humans and apes had already topological transformations in the area of the liver, towards allowing the supply of energy through ketosis, of particular importance later on to larger brains under more carnivore diets. It is possible that the capacity to synthesize vitamin C in humans, which is also common to the apes, was lost at that time.

b) Between 3.0 and 2.5 m.y., topological transformations in the endocrine area of gracile autralopiths, produced robust forms of australopiths, which became extinct around a million years ago.

c) Another set of topological transformations involving a different deme of gracile autralopiths, occurred around 2.5 and 2.0 m.y., affecting principally the brain, and endocrine areas (particularly circumventricular glands such as the pineal). A trend of topological transformations towards smaller molariforms started here and is still in progress. This yielded demes of protohumans of the *habilis* grade. At this time the brain probably passed the threshold platform of organization that could epigenerate a mind, and therefore sustain cultural algorithms. This facilitated population increase under a more energy demanding niche (the proportion of brain size to body size is proportional to energy consumption).

d) Between 2.0 and 1.0 m.y. the remaining gracile autralopiths became extinct.

e) Another set of topological transformations around 1.5 million years ago, principally again in the endocrine area, promoted anatomical allometric enlargement and probably a syndrome of other changes already started at the *habilis* grade, for example on teeth, skin, sexual area, and maturation/longevity (with their respective consequences on the mind, and complexification of cultural algorithms). These "mesohumans" were of the *erectus* grade. They expanded to Eurasia during the next million years, forming polymorphic and polytypic populations.

f) Between 0.5 and 0.2 m.y. the record is not clear, but it is possible that many of the different demes of the *erectus* grade became extinct, perhaps leaving relicta here and there, or anastomosed in large extent ("reticulate evolution") as suggested by Tobias (1983). Probably around 120-100 thousand years B.P., from the demes of a pre-sapiens form that thrived, and by continuing the trend of topological transformations on the endocrine and brain areas, "neohumans" of the early *sapiens* grade evolved and expanded again in the Old World.

g) Topological transformations again, principally in the endocrine area of some early *sapiens*, produced in Europe the forms of Neanderthal grade ("classic"), which became extinct around 40-30 thousand years ago.

h) Between 50-30 thousand years B.P., topological transformations on endocrine epigenetic chains involving another set of of early *sapiens* individuals triggered

paedomorphic changes (neoteny) towards the more gracile forms of modern humans, which became rapidly dominant, as a result of more successful cultural algorithms and probably a more efficient overall mind.

i) As in all other grades of human evolution the populations that expanded were highly polymorphic. Genetic drift probably played an important role in differentiating demes at the time of expansion (rarefaction). Around 10,000 B.P. the different aspects of the mesolithic-neolithic revolution brought about the differential expansion of the most successful food collector-producers in different spaces of the Ecosphere, creating an intricate polymorphic-polytypic mosaic, made even more complex during historical times. In some other instances, isolation (e.g. Australia) contributed to add variety to the total picture.

Analogies between biological and cultural evolution are not granted because they are two very different processes. The only similarity is that cultural evolution also involves change (in cultural algorithms) through space and time. However, cultural evolution has strong non-random determinants, and synformation from other cultural algorithms (**acculturation**) not present in biological evolution. Biological evolution under culture is also guided by determinants such as domestication, intentional alteration of probabilities of extinction, and biotechnology.

On the other hand, the evolution of the mind could have been parallel to the topological transformations of the brain area, with each one of the thinking modes becoming more effective at each step of human evolution. Speculatively: algorithmic thinking has assumed importance at the *habilis* grade, and continues to improve efficiency towards modern man; successional epigenetic thinking the same starting at the *erectus* grade; and non-successional epigenetic thinking at the *sapiens* grade.

In the case of human evolution only the general guidelines presented above are possible at the present state of knowledge. A more detailed illustration of the application of the theory of topological transformations and jumps, requires the analysis of empirical data from simpler structural units. The different forms of bioliths provide ideal materials for such endeavor. In chapter 2, biosilica phytoliths are used to support conformity with this theory.

Niche components correlate among themselves and also with other ecosystem components, because they contain redundancy principally related to coupling. Therefore, it is possible to estimate somatoniches, and at least attempt partial reconstruction of paleoecosystems by analysis of redundant information (**proxy data**) from **fossils** (coded information about components of extinct niches). A similar task can be performed using information coded on abiotic components (e.g. geochemistry, geophysics). Spurious correlation generated by random variation (pure variation

redundancy), distortion, noise, or interference (e.g. diagenesis, taphonomic scrambling), can be minimized by cross correlation, i.e. verifying redundancy in common. Paleoecosystemic models are thus improved by combining multivariate decoding methods, to augment information and diminish errors. Multivariate evaluations also help identifying non-redundant variation among components. In chapter 3, phytoliths are again used to illustrate these points, and provide novel information about Beringian ecosystems. Finally, in Note 5, the effect of different rates of epigenetic transition in evolutionary extinction, is used to explore the causes for the faunal changes during the Pleisto-Holocene mesoglacial in the New World.

NOTE 2: A condensed biography of Ehrenberg

Christian Gottfried Ehrenberg was the founder of phytolith analysis (actually of micropaleontology).

Ehrenberg was born in Delitzsch, near Leipzig, Germany, 19 April 1795, and died in Berlin, Germany, 27 June 1876. He studied medicine in Leipzig and Berlin, attending at the same time courses and lectures in zoology, botany, and geology (he always believed in multidisciplinary education), receiving a Doctor of Medicine degree in 1818, with the presentation of a botanical dissertation on fungi from the vicinity of Berlin. In this work he showed for the first time the development of fungi from spores, pioneering and employing intensely microscopical techniques, which lead him to become one of the most accomplished microscopists of his time. His monumental descriptive work with the microscope includes for example, the formation of the pollinic tube, and the discovery of thousands of bacteria (he actually created the name *Bacterium*), diatoms and other algae, protozoan, and many other biogenic structures, living and fossil, such as phytoliths. Other notable accomplishments were the first exact investigations on the anatomy and physiology of corals, the explanation of sea phosphorescence, and many other pioneering researches in biological oceanography (including analysis of sea bottom sediments), and limnology.

Ehrenberg was made Extraordinary Professor of the University of Berlin in 1827, and Professor of Medicine in

1839, but although he belonged to the medical faculty, his lectures and demostrations were mainly on botany, zoology, and geology, and almost devoid of direct medical interest. In 1827 Ehrenberg was elected a member of the Berlin Academy of Sciences, and later of many other European academies. Although he helped many students when asked, Ehrenberg never had formal graduate students, and always preferred to do his work alone. However, he was an incredibly productive scientist, publishing copiously on botanical, zoological, anthropological, histological, geological, geographical, meteorological, archaeological, and physiological subjects, among others. For 30 years starting in 1841 Ehrenberg produced many papers in which he described phytoliths from worldwide soils, sediments (including marine), and dust. Most of them appeared in the publications of the Berlin Academy of Sciences. His main book on the subject, and other microfossils, was Mikrogeologie published in 1854 with a supplement in 1856.

Ehrenberg participated in two major scientific expeditions. One very perilous to Egypt, Lybia, Sudan, Sinai, and Arabia, particularly exploring the Red Sea; and another with Alexander von Humboldt to Russia and Siberia. In addition to his own collections, being a friend of many notable naturalists of his time, such as von Humboldt and Darwin, he received many samples of soils and sediments from all over the World, which formed the base for his wide ranging micropaleontological studies. His collections and

manuscripts are still available at the Museum für Naturkunde in Berlin.

His microscopic observations were all made on a 300X microscope, which he bought when young. As a curiosity, it is interesting mentioning that he always made his very long microscopic observations standing up. A more important historical fact is that he always refused to use more powerful and optically better instruments, available later on in his career. This could have helped to improve considerably his tireless observations. Stubborness was a dominant trait of his personality. For example, before the cellular theory was proposed, he thought that all animals, including protists, possessed the same organs, forming nervous, digestive, vascular, sexual, and muscular systems, which he used as an argument against the theory of spontaneous generation and the "chain of being." After it was demonstrated that only multicellular organisms have organs, and that protists were unicellular, he continued to defend his views for a long time. Also, he never accepted biological evolution. Nevertheless, his errors cannot eclipse his innumerable contributions to Science, a fact actually recognized during his lifetime by the many medals, prizes, and honors received from the major learned societies and academies of Europe at that time.

On a personal note, he was a very nice man and loyal friend, and also something of a poet as well as an accomplished draughtsman. He married the niece of the german

mineralogist Gustav Rose, Julie Rose, in 1831. From this marriage he had one son and four daughters. After the early death of Julie (1848), he was married again, in 1852, to Karoline Friederike Friccius, sister-in-law of the chemist Eilhard Mitscherlich, and had no further progeny. Ehrenberg's youngest daughter, Clara, aided her father in his scientific research to the end of his life, even making microscopic observations for him, when both of his eyes were afflicted with cataract.

A very comprehensive biography of Ehrenberg, including a bibliography, was prepared by Laue (1895).

NOTE 3: Phytolith synonymia

A large number of synonyms for phytolith have proliferated in the literature, difficulting communication and bibliographic searches. This is a minimum list of such synonyms in the languages of the available literature. Some terms are imprecise or technically wrong, but that is the way they were employed in the literature. Most common synonyms in English are marked with an asterisk.

Biogenetic or biogenic opal (English).

Biogenetic or biogenic silica (English).

Cellule silicieuse (French).

Células silíceas or silicificadas (Spanish, Portuguese).

Cône silicieuse (French, for sedge phytoliths).

Concretion silicieuse (French).

Corpo silicoso (Portuguese).

Crown cells (English, for short trichome spiny phytoliths).

Cuticle silica (English).

Epidermal opal or silica (English).

Excrétion silicieuse (French)

Fitolita (transliterated Russian).

Fitoliti (Italian, transliterated Bulgarian).

Fitolito or Fitólito (Spanish, Portuguese).

Grass opal (English).

Kieselerde (German).

Kieselkörpe (German).

Kieselmembran (German).

Kieselsäure (German).

Kieselskelett (German).

Kieselzellen (German).

Opal body* (English).

Opaline silica (English).

Opalo organógeno (Spanish).

Phytolite (English).

Phytolith* (English).

Phytolithaire (French).

Phytolitharia (Latinized name).

Phytolithe (French).

Plant biolith (English).

Partículas de sílice organizada (Spanish).

Plant opal or silica* (English).

Plant silicon (English).

Sedge opal (English).

Sílica biogênica (Portuguese).

Silica body* (English).

Silica cell (English).

Silica or opal corpuscle (English).

Silica cystolith (English).

Silica or opal particles (English).

Silica or opal sand (English).

Silica or silicified sclerite (English, usually for tree phytoliths).

Sílice biógena (Spanish).

Silicified asterosclereid (English, usually for conifer phytoliths).

Silicified atherosclereids (English, wrong version of the prior one).

Silicified cell (English).

Silicofitolito (Spanish).

Silicophytolith (English).

Stegmata (German, English, for palm phytoliths).

There is a considerable literature on phytoliths in Japanese; however, it generally uses a direct translation of the English synonyms.

There is considerable literature on phytoliths in Japanese; however, it generally uses direct transliteration of English synonyms.

NOTE 4: Carbon isotopes in paleobiology

Photosynthetic fixation of carbon dioxide by terrestrial plants produces a change in the $^{13}C/^{12}C$ ratio, because of discrimination against the heavier isotope. These changes in carbon isotope ratios are conventionally reported in the $\delta^{13}C$ notation, which expresses the relative content of ^{13}C in relation to the Chicago PDB standard (carbonate from the Cretaceous marine fossil *Belemnitella americana*, from the Pee Dee Formation of South Carolina) in parts per thousand (per mil or $^{o}/_{oo}$), according to the relation: $\delta^{13}C$ per mil = $[(\text{sample } ^{13}C/^{12}C)/(\text{PDB } ^{13}C/^{12}C) - 1] \times 10^{3}$. The original PDB standard is no longer available, but all laboratories relate to it through secondary standards.

Uncontaminated atmospheric CO_2 has a $\delta^{13}C$ of about -7 per mil, while plant carbon can have values as much as 30 per mil lower. The extent of this fractionation depends on metabolism and environment; however, from all the species analyzed so far, the natural distribution of $\delta^{13}C$ throughout the Plant Kingdom is bimodal, and related to the respective photosynthetic pathway. Plants with the C_3 pathway, which initially fix CO_2 in 3-carbon acids by carboxylation of ribulose biphosphate (Calvin cycle), have $\delta^{13}C$ ranging from -37 to -21 per mil (average -26.5 per mil). Those with the C_4 pathway, which initially fix CO_2 in 4-carbon acids by the carboxylation of phosphoenolpyruvate, have $\delta^{13}C$ ranging from -19 to -8 per mil (average -12.5 per mil). Plants with crassulacean acid metabolism (CAM) can be functionally

equivalent to C_3 if they fix carbon during the day, or to C_4 if they fix it during the night (generally in response to xeric conditions); therefore, their $\delta^{13}C$ depends on environmental factors, and cover the range of values for C_3 and C_4 plants, including intermediate ratios. Ground level CO_2 in dense forests has $\delta^{13}C$ values more negative than in open air, due to carbon recycling through litter decomposers, and this will be reflected throughout the trophic levels.

The distribution of plants with the three different photosynthetic pathways is not homogeneous throughout terrestrial ecosystems. Most trees, shrubs, and temperate/arctic graminoids are C_3 plants. Tropical grasslands, or mid-latitude xeric/saline and well irradiated environments, commonly have a considerable proportion of C_4 species. CAM plants are typically tropical or warm temperate succulents, particularly adapted to arid/semi-arid climates. Transects through environmental gradients have shown characteristic changes in the proportions of C_3 to C_4 plants. Therefore, the proportions of C_3/C_4 fixed carbon in fossil assemblages, as measured by their $\delta^{13}C$, can be used as paleoenvironmental indicators. $\delta^{13}C$ of herbivore feces or gut content estimate well the proportion of C_3 and C_4 in their diets, providing information on vegetation selectivity by herbivores, proportion of grazing/browsing, and niche overlap.

Temperate cultivated plants are usually C_3, but some important cultivars, such as maize, sorghum, and sugar cane, are C_4. $\delta^{13}C$ of marine CO_2 is enriched by about 7 per mil in relation to air, and this is reflected in the marine food chains. Excluding plankton, marine plants have C_4-like ratios. These differences have applications in archaeological, and geoenvironmental studies.

Despite additional fractionations when carbon is transferred from the producers through food webs, the consumers being generally enriched in ^{13}C, it has been demonstrated that the animal tissues (including bone) will reflect, proportionally, the isotopic ratio signatures of the respective diets. This property has been applied to determine present trophic relationships, and archaeological subsistence strategies. A fully referenced review of the subject of carbon isotopes in paleobiology is presented by Bombin and Muehlenbachs (in press).

NOTE 5: Mesoglacial megafaunal extinctions in Beringia and the Americas

Presently published models for the extinction of megafauna in the New World, during the mesoglacial, are usually mono-causal (see review by Bombin, 1980a), and therefore fail to accomodate all the evidence, which is multivariate. However, it is possible to produce a more realistic and unified model that accounts for the extinction of Beringian and the other American Pleistocene megabeasts, their natural predators, specialized scavengers, and obligatory feeding successors, between 15,000 and 8,000 BP. Instead of considering isolated causes (e.g. overkill or climatic hypotheses), the model integrates environmental, anthropogenic, and paleobiological processes in a feedback system that causes a continuous change in the probability of extinction of megamammals, when parameters are changed.

The probability of extinction of organisms is increased by any (or combinations) of the following situations:

- inadequacy of the ecosystem to provide energy-matter requirements;

- ineffective coupling between niches and environmental matrix;

- incompetence to adapt (change niche channels) to changing environments;

- inability to sustain competition (trophic and/or territorial);

- constrains to cope with predation;
- interfering catastrophic events.

For each particular case there is a singular set of processes through which the aforementioned reasons are effected. Therefore, to produce an explanatory model for the synchronous extinction of a set of different organisms, it is necessary to integrate redundant processes that can produce the situations listed above at the same time. Also, because different organisms have different probabilities of extinction, if they go extinct at the same time there is only a very remote probability of that happening by random chance. The reason is likely some redundant property of the extinct set. Conversely, the same is true for the set that survived.

A summary of redundancies present in the case of mesoglacial megafaunal extinctions in Beringia and the Americas includes:

1) The time of probability of extinction increase for all organisms involved was between 15,000 and 8,000 BP, and probably peaking between 12,000 and 10,000 BP.

2) Table 1 provides statistics on New World extinct and survivor megafauna (humans excluded), showing redundancy in size. Important features to consider here are:

a) The extinct megafauna was predominantly adapted to open canopy vegetation systems.

b) Pre-extinction faunas (extinct + survivors) show a greater diversity of grazers and browsers, suggesting

Table 1 - Late Quaternary Megafaunas of the New World

North American Holoarctic			Neotropics		
Survivors	gen.	kg	Survivors	gen.	kg
capybara	1	25-50	capybara	1	25-50
pronghorn	1	35-65	vicuña	1	50
wolf	1	25-75	pampa deer	1	30-60
puma	1	35-100	huemul	1	40-60
jaguar	1	70-100	white-tail deer	1	30-80
white-tail deer	1	50-90	giant armadillo	1	50-60
sheep	1	35-125	puma	1	35-100
goat	1	80-120	guanaco	1	70-90
mule deer	1	100-110	jaguar	1	70-100
black bear	1	120-200	marsh deer	1	90
caribou	1	120-300	spectacled bear	1	120-130
wapiti	1	125-320	tapir	1	250
musk-ox	1	270-400		11-12	85±15
griz./brown bear	1	200-700			
polar bear	1	300-700			
moose	1	400-650			
bison	1	450-1300			
	16	250±100			
Extinct			Extinct		
saiga	1	50	peccaries	1-2	50-100
pronghorns	2	10-100	capybara	1	100-150
peccaries	2	50-100	pampathere	1	100-200
cervids	1-2	100	cervids	2-4	100-250
capybara	1	100-150	camelids	2	100-250
shrub-ox	1	130	sabre-tooth cat	1	150-250
pampathere	1	100-200	horses	3	250-350
giant beaver	1	180-200	short-face bear	1	200-400
sabre-tooth cat	1	150-250	giant tortoise	1	300-500
scimitar cat	1	150-250	macrauchenia	1	400-600
camelids	2-4	100-500	glyptodonts	9	100-1000
tapir	1	250	ground-sloths	9	200-5000
lion	1	250-300	toxodont	1-2	2000-3000
horses	1	250-400	mastodonts	1-3	3000-5000+
glyptodonts	1-2	200-600		35-40	850±350
giant tortoise	1	300-500			
musk-ox	1	350-500			
yak-like bovid	1	500			
short-face bear	1-2	300-800			
giant moose	1	1000			
ground-sloths	4	200-3000			
mastodonts	2	3500-5000+			
mammoths	1	3000-6500+			
	30-35	750±250			

environmental diversity within their migratory radius. In fact, recent big mammal faunas of the American tundras/sedge meadows, or grasslands, are clearly impoverished in comparison to the Pleistocene, and have generally large populations of a few species, with smaller individuals than the past counterparts.

c) High proportion of preferential grazers became extinct.

d) Survivors are well adapted to zonal environments (less heterogeneous within habitat).

e) Most extinct forms have no ecological vicars among survivors.

f) There is a higher proportion of ruminants (more efficient large herbivores) among survivors.

g) Predators of giant forms were rare in Beringia and the rest of the New World. In the Neotropics, for example, sabre-tooth cats were very rare.

h) Only a few genera with more than 100 kg survived (only two in the Neotropics).

i) Adaptive characteristics of the survivors include:

- herbivores with preference or adaptive capacity for living in forests or ecotones between forests and open vegetation (e.g. tapir, peccaries, spectacled bear, some deer); high mountain habitats (e.g. sheep, goat, vicuña); arctic and boreal forest environments (e.g. caribou, moose, musk-ox); xerophytic homogeneous habitats (e.g. guanaco, sheep, pronghorn); homogeneous grasslands (e.g. bison,

pronghorn, guanaco, and some deer); marshy lands (e.g. marsh deer, moose, capybara).

- Carnivores adapted to hunt a wide range of prey sizes, generally small to medium (e.g puma, jaguar, wolf), or trophically related to the talassocycle (e.g. polar bear);

- Highly competitive omnivores (e.g. black and grizzly bears). All of these were effective or beneficial within the post-glacial environmental matrices.

3) The recurrence and persistence of diverse giant forms ("K-strategists") throughout the Pleistocene, suggests an overall dynamic environmental predictability during most of this epoch. By comparison with present "K-strategist" faunas, where the rate of ontogenic transition is low, it is licit to assume that the organisms in Pleistocene megafaunas had niches including the following redundant features: slower ontogenic development towards large size, use of energy emphasizing maintenance and efficiency instead of reproduction and productivity, delayed and repeated reproductions during long and complex life cycles, long dependence of young, and elaborated behavior and social organization. This was primarily due to allometric probabilities correlated with large-sized animals, such as lower intrinsic rate of natural increase, metabolic rate/weight ratio, secondary productivity/standing biomass ratio, descendants/time ratio, birth rate, litter size and frequency; longer generation time, lifespan, life expectancy

at birth, age at first parturition, gestation time, birth interval; and higher absolute food intake and territorial requirements.

The dominance and persistence of this life strategy indicates communities tending to be saturated, with uncommon recolonization, and population sizes fairly constant in time (close to the carrying capacity of relatively predictable environments). This requires successful keen intraspecific and interspecific competition (trophic and territorial), because of assymptotic biomass and high diversity, which increases the probability of niche specialization. Under these circumstances, there is a tendency to develop well organized stratification and spatial heterogeneity (pattern diversity), and high degree of integration of the feeding and territorial strategies (symbiosis and mutualism), as well as faunal influence in generating or improving their own habitats. The well developed and intricate feedback web in such systems tends to maximize homeostasis under relatively predictable (ergodic) conditions; therefore, the demes have long lasting "memory" about negative stochastic effects upon reproductively active individuals, which below a certain number lose the ability to maintain a viable population (at this threshold the probability of extinction = 1). Recent animals close to this threshold are for example the whooping crane and the blue whale.

4) Noteworthy environmental changes occurred during the time of the extinctions. Areas becoming free of glacial ice

were constantly being made available for colonization, for example, areas where Laurentide ice was waning were rapidly colonized mainly by boreal forests and wet tundra. Considerable extensions of land were transgressed by the postglacial eustatic rise of the oceans, diminishing the continental areal capacity of supporting megafauna (important factor in Beringia), but also reducing possibilities of migratory transit, altering hydrologic characteristics, and coastal resources. During the peak of the extinctions, considerable areas of North America were still under glacial ice.

In the unglaciated portions of eastern Beringia, the climate became less continental, and extensive diverse steppes, lowland meadows and willow shrublands, gave way to wet tundra and boreal forest. At the same time, in eastern North America, the open conifer forests and parklands, and the oak-shrub-grasslands, were succeeded by close canopy forests, at the same time that coastal lowlands became permanent marshlands. Some areas of the Great Plains and the Pampas probabily improved the graminoid range and productivity (particularly after humans started intentional burning); however, there was an overall loss of diversity and heterogeneity. In the tropical areas, particularly in the Amazon Basin, former extensive open canopy areas were very significantly reduced by closed pluvial forests. The total reduction in area suitable to sustain diverse megafaunal communities, and for its migratory transit, by

submersion, forestation, desertification (e.g. Atacama, Great Basin), was of the order of 50%.

Considering all these mesoglacial changes, the period when the bulk of the megafaunal extinctions occurred was chacaterized by enormous environmental variability, and continuous ecological readjustments to the postglacial regime. This included a previously absent and powerful variable: the arrival, adaptations, and demographic expansion of humans.

5) To be able to expand into Beringia at the peak of last glacial, or the beginning of the mesoglacial, humans had to be very skilled big-game hunters, otherwise they would have not survived there. The same is true for the people that came south through the ice-free corridor. Therefore, the first paleo-indians were, in my opinion already adapted to hunting megafauna. Other adaptations, such as generalized gathering and hunting developed later in America. The same is the case of maritime adaptations. I do not think that a Pacific coastal route was hospitable or even feasible during the early mesoglacial.

Between 12,000 and 11,000 BP humans were already inhabiting practically all possible available habitats in the Americas, hunting and interfering ecologically with megafauna from Beringia to Patagonia.

From the previous summary, there is ground to propose that all the situations that increase the probability of extinction of organisms, listed at the beginning, were in

effect in one way or another at the time the megabeasts vanished. Therefore, there is no reason to single out any particular cause for the extinctions. It makes ecologically and evolutionarily more sense to model this episode as a resultant of the combined effect of interrelated processes, conducive to make the probability of extinction of megamammals tend to 1.

Most of these suggested processes and interrelations are synthesized in Figure 23.

It is possible that this kind of model, with proper modifications, would find application to explain extinctions of "K-strategists" in other space and time contexts.

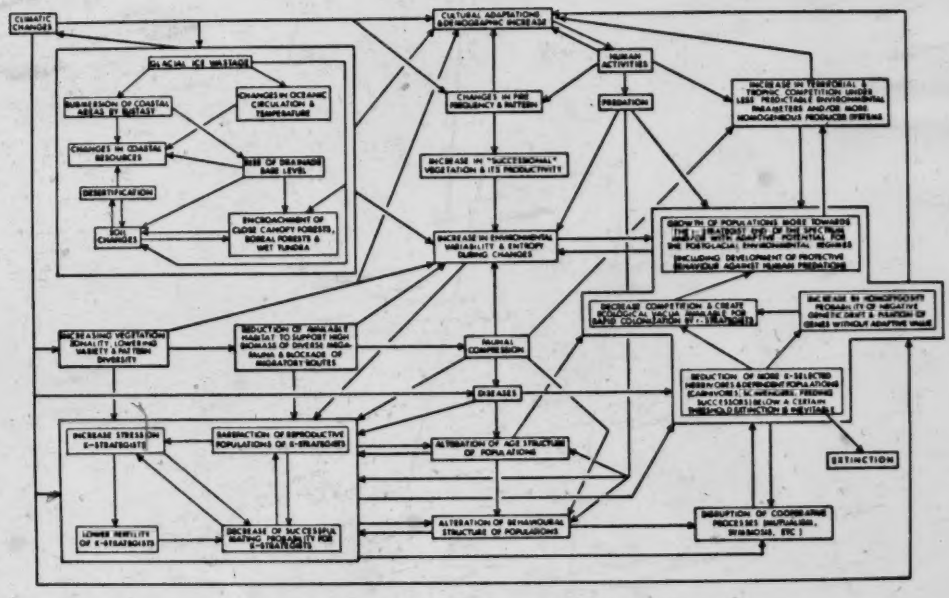

CLIMATIC CHANGES
CULTURAL ADAPTATIONS & DEMOGRAPHIC INCREASE
GLACIAL ICE WASTAGE
SUBMERSION OF COASTAL AREAS BY EUSTASY
CHANGES IN OCEANIC CIRCULATION & TEMPERATURE
CHANGES IN COASTAL RESOURCES
RISE OF DRAINAGE BASE LEVEL
DESERTIFICATION
ION CHANGES
ENCROACHMENT OF CLOSE CANOPY FORESTS, BOREAL FORESTS & WET TUNDRA
INCREASE IN ENVIRONMENTAL VARIABILITY & ENTROPY DURING CHANGES
CHANGES IN FIRE FREQUENCY & PATTERN
INCREASE IN "SUCCESSIONAL" VEGETATION & ITS PRODUCTIVITY
HUMAN ACTIVITIES
PREDATION
INCREASE IN TERRITORIAL & TROPHIC COMPETITION UNDER LESS PREDICTABLE ENVIRONMENTAL PARAMETERS AND/OR MORE HOMOGENEOUS RESOURCE SYSTEMS
GROWTH OF POPULATIONS MORE TOWARDS THE [illegible] END OF THE SPECTRUM AND LESS ABLE TO EXPLOIT POTENTIAL FOR ENVIRONMENTAL REGIMES POSTGLACIAL
INCLUDING DEVELOPMENT OF PROTECTIVE BEHAVIOUR AGAINST HUMAN PREDATION
INCREASE COMPETITION & CREATE ECOLOGICAL VACUA AVAILABLE FOR RAPID COLONIZATION BY r-STRATEGISTS
INCREASE IN HOMOZYGOSITY PROBABILITY OF NEGATIVE GENETIC DRIFT & FIXATION OF GENES WITHOUT ADAPTIVE VALUE
INCREASING VEGETATIONAL ZONALITY, LOWER PRODUCTIVITY & PATTERN DIVERSITY
REDUCTION OF AVAILABLE HABITAT TO SUPPORT HIGH BIOMASS OF DIVERSE MEGA FAUNA & BLOCKADE OF MIGRATORY ROUTES
FAUNAL COMPRESSION
DISEASES
REDUCTION OF MORE K-SELECTED HERBIVORES & DEPENDENT POPULATIONS (CARNIVORES) TO MINIMUMS FEEDING SUCCESSORS BELOW A CERTAIN THRESHOLD DISTINCTION & INEVITABLE
INCREASE STRESSES ON K-STRATEGISTS
DISRUPTION OF REPRODUCTIVE POPULATIONS OF K-STRATEGISTS
ALTERATION OF AGE STRUCTURE OF POPULATIONS
EXTINCTION
LOWER FERTILITY OF K-STRATEGISTS
INCREASE OF SUCCESSFUL MATING PROBABILITY FOR K-STRATEGISTS
ALTERATION OF BEHAVIOURAL STRUCTURE OF POPULATIONS
DISRUPTION OF COORDINATE PROCESSES (MUTUALISM, SYMBIOSIS, ETC.)

Figure 23 - Processes altering the probability of extinction of the American mesoglacial megafauna.

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APPENDIX 1: Sample of a phytolith analysis protocol sheet

1. Morphotype # : Linnean Taxon:
2. Sample material, provenance:
3. Processing, mounting:
4. Microscopy data:

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5. Summary description:

---

6. Mother-cell:
7. Tridimensional shape:
8. Upper view shape:
9. Lateral view shape:
10. Frontal view shape:
11. Length:
12. Width:
13. Height:
14. Side morphology:
15. End morphology:
16. Crest:
17. Keel:
18. Processes:
19. Vacuoles:
20. Transparency, staining:
21. Preservation:

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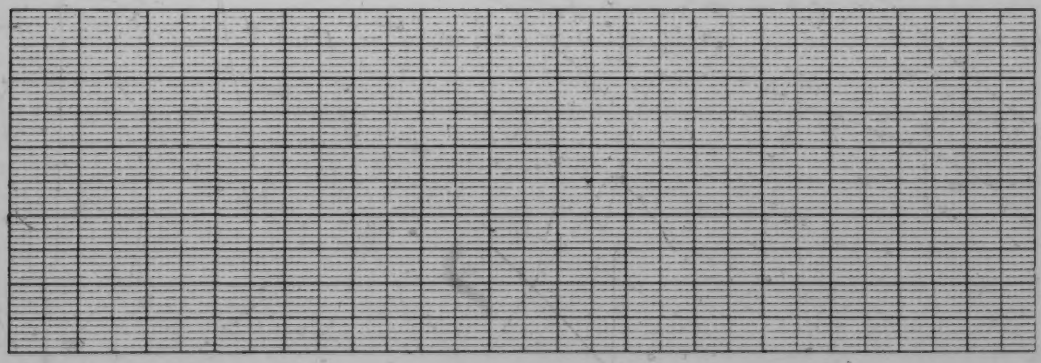
22. Observations, references:



Analyst: Date: